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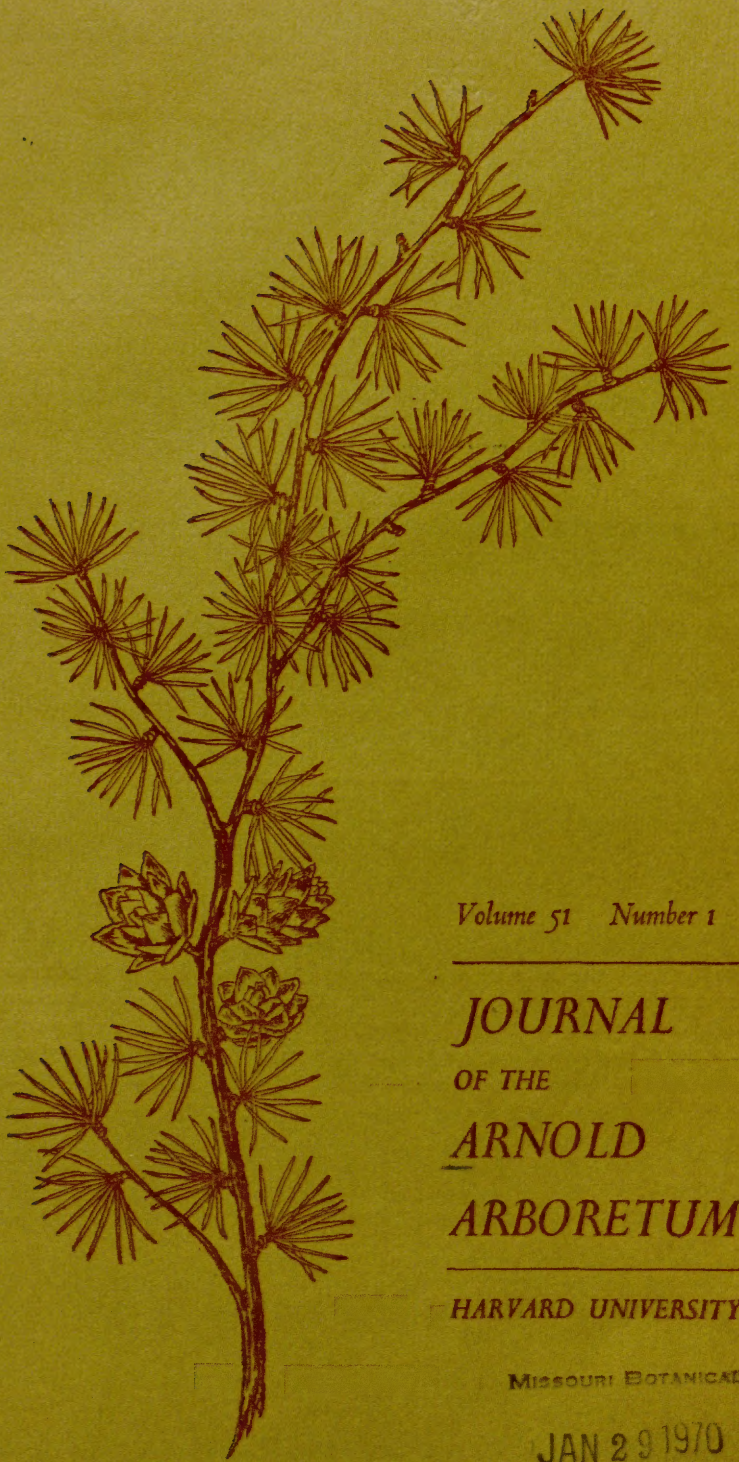

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COVER: The Golden Larch, *Pseudolarix* Gordon

WITH volume 51 the *Journal of the Arnold Arboretum* begins its second half century of continuous publication. To celebrate the occasion we are pleased to present a new cover format. The cover design is the work of Norman Comeau of the Art Department, Thomas Todd Company, Printers, Boston. We hope from time to time to have drawings of other plants on the cover. The Table of Contents will appear on the back cover. *Eds.*

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THE SYSTEMATICS AND BREEDING SYSTEM OF GELSEMIUM (LOGANIACEAE)

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ROBERT ORNDUFF

THE LOGANIACEOUS GENUS *Gelsemium* exhibits a pattern of distribution that has interested plant geographers and systematists for over a century (Gray, 1846, 1859; Hara, 1952, 1956; Miranda & Sharp, 1950; Li, 1952). The genus is represented by one species in southeastern Asia, a second species in the southeastern United States, and a third species in the southeastern United States and the highlands of southern Mexico and Guatemala. This distribution pattern is similar to that which occurs in a number of other taxa of flowering plants. Although this disjunction dates back to the close of the Tertiary, *Gelsemium* has continued to maintain a relatively high degree of morphological and genetic homogeneity. The purpose of this paper is to present a general systematic account of *Gelsemium* and to discuss the breeding system which is associated with heterostyly in the genus.

I am indebted to D. E. Breedlove, J. F. M. Cannon, S. C. K. Chan, J. E. Ewan, R. K. Godfrey, A. Lourteig, L. I. Nevling, Jr., G. B. Newcomb, W. T. Stearn, and G. L. Webster who assisted this study in various ways. I am also grateful to the National Science Foundation, whose grants have provided financial support for this investigation. The paper was written during the tenure of an appointment in the Miller Institute for Basic Research in Science at the University of California. Specimens deposited at A, BM, DUKE, E, F, FSU, GH, K, LAF, MISSA, MO, NCU, NO, NSC, NY, SMU, UC, and USF have been examined and I am grateful to the staffs of these herbaria for making the specimens available to me.

RELATIONSHIPS

The relationships of *Gelsemium* ($n = 8$, see below) to other genera of Loganiaceae are not at all clear. In their description of the Asian species in 1849, Gardner and Champion suggested an affinity with the African *Usteria* ($n = 11$; Miège, 1960) and the South American *Antonia* based on similarities of capsule structure. Bentham (1876) placed *Gelsemium*,

the African-South American *Mostuea* ($n = 10$; Gadella, 1962, 1963), and the Central American *Plocosperma* together in the tribe *Gelsemieae*. The occurrence of distyly (Leeuwenberg, 1961) and indole alkaloids (Leenhouts, 1962) in both *Gelsemium* and *Mostuea* supports the morphological evidence indicating that these genera are allied, but the cytological data do not conclusively support this affinity. Moore (1947) indicated that *Gelsemium* has an isolated position in Loganiaceae and might have closest affinities with Apocynaceae, although he favored retention of the genus in the first family.

Despite the number of generic names that have been applied in *Gelsemium*, the only attempt to discriminate between New World and Asian species at the generic level was that of Gardner and Champion, who distinguished the Asian *Medicia* from *Gelsemium* because the former has "imbricated, not quincuncial, aestivation of the corolla, inflated capsule, and numerous peltate, compressed seeds surrounded on all sides by a broad inciso-dentate membranous wing." The differences in aestivation are slight and the seeds of *G. sempervirens* are asymmetrically winged, thus leaving the capsule character as the sole one which might be used for a generic distinction. I am, therefore, inclined to follow the tradition of other workers in recognizing only a single genus. Nevertheless, the Asian species is considerably more different from the two American species than these are from each other.

Chromosome numbers of $2n = 16$ have been obtained for the three species of *Gelsemium* (TABLE 1; Moore, 1947; Gadella, 1963). All chromosome counts reported in this paper were made on mitotic tissue of shoot apices with the exception of a single meiotic count obtained from microsporogenous tissue in *G. sempervirens*. Recently Duncan and DeJong (1964) have reported $2n = 8$ for *G. rankinii* based on sectioned material in which counts of $2n = 9$, 10, and 16 were also noted. Because of the variation in the number of chromosomes they observed, the difficulties in interpreting sectioned material (see, for example, Epling, Lewis, & Raven, 1962), and the consistent chromosome number of $2n = 16$ that I have obtained for this species from several localities, Duncan and DeJong's report and the evolutionary conclusions based upon it are open to question.

Attempts to produce artificial hybrids from legitimate crosses between *Gelsemium sempervirens* and *G. rankinii* resulted in low seed production (TABLE 2). All hybrid seed was planted, but the germination percentage was also very low. A total of eleven hybrid plants has been obtained, but these are considerably less vigorous than seedlings of the parental species. Most of the hybrids died a few months after germination and the remainder have been slow to produce flowers. The only hybrid which has flowered is one individual obtained from a cross between *Breedlove 9005* (*G. sempervirens*, Chiapas, Mexico) and *Godfrey 62671* (*G. rankinii*, Liberty County, Florida). This plant produced a single flower with pollen having an 81% viability, based on the stainability of a sample of 200 pollen grains mounted in aniline blue-lactophenol. However, when it was

backcrossed to both parents only five seeds matured in the capsule. In pedicel, sepal, and capsule characters the hybrid resembled *G. rankinii*, but the winged seeds were similar to those of *G. sempervirens*. Thus, these two species are separated by barriers to crossing, by low germinability of hybrid seed, and by reduced viability and fecundity of the hybrids.

Some plants of the Guatemalan and Mexican populations of *G. sempervirens* are indistinguishable from those in the United States, but others have leathery, dark green, glossy, involuted leaves, as well as a tendency for higher numbers of flowers in each inflorescence. In addition, these Meso-American plants apparently have unscented flowers, whereas flowers of this species in the United States have a very strong fragrance.

TABLE 1. **Chromosome numbers of Gelsemium**

COLLECTION DATA	LOCALITY	CHROMOSOME NUMBER
G. SEMPERVIRENS:		
L. E. Anderson, s.n.	Durham County, North Carolina	$n = 8$
Ornduff 6376	Hoke County, North Carolina	$2n = 16$
Ornduff 6707	Richland County, South Carolina	$2n = 16$
Breedlove 9005	Pueblo Nuevo Solistahuacán, Chiapas, Mexico	$2n = 16$
G. RANKINII:		
G. B. Newcomb, in 1965	Tammany Parish, Louisiana	$2n = 16$
R. Godfrey 62667	Liberty County, Florida	$2n = 16$
R. Godfrey 62671	Liberty County, Florida	$2n = 16$
R. Godfrey 62673	Franklin County, Florida	$2n = 16$
G. ELEGANS:		
S. C. K. Chan, s.n.	Hong Kong	$2n = 16$

A few hybrids have been obtained from a cross between some plants of *G. sempervirens* from Chiapas, Mexico, and others from Durham County, North Carolina. These parental populations are from the extreme ends of the range of this species. The pollen viability of the two hybrid plants that have flowered at the time of writing is 100% (based on a sample of 100 grains mounted in aniline blue-lactophenol). This suggests that the somewhat divergent morphological and biochemical characters (i.e., lack of flower odor) of the geographically disjunct parental populations are not associated with sufficient genetic discontinuities to result in lowered pollen viability of hybrids obtained from a wide geographical cross.

TOXIC PROPERTIES

The herbage of *Gelsemium* contains several toxic alkaloids (Debay, 1950; Martínez, 1959; Kingsbury, 1964). *Gelsemium sempervirens* causes death and abortion in livestock which feed upon its leaves (Hardin, 1961; Kingsbury, 1964). Ingestion of nectar and honey produced from *Gelse-*

mium flowers reportedly has caused death in humans and bees in the southeastern United States (Kingsbury, 1964). Information concerning *G. elegans* indicates that this species has been used in China, Viet Nam, and Borneo as a suicidal poison which is either ingested or smoked. A note with *Khant 15216* (K) states that this species is used as a fish poison in Burma. The label of *Dickason 9789* (GH) reports that the flowers of *G. elegans* are "poisonous to smell! Kills butterflies on the flowers." It has been stated (*Gibbs* in 1910, BM) that in Borneo this species is "much used for feeding pigs . . . but is very poisonous to man."

Despite its toxic properties, *Gelsemium sempervirens* is frequently grown in the gardens of the southeastern United States and of California, where it is prized for its heavily fragrant yellow flowers. It has been cultivated in Europe since the mid-17th century.

TAXONOMY

Gelsemium Jussieu, Gen. Pl. 150. 1789.

Jeffersonia Brick., Med. Rep. N.Y. 1: 555. 1800.
Medicia Gardn. & Champ., Hook. Jour. Bot. 1: 324. 1849.
Leptopteris Blume, Mus. Bot. Lugd. Bat. 1: 240. 1850.

Type species: *G. sempervirens* (L.) Jaume Saint-Hilaire.

Twining woody vines; leaves opposite, simple, entire, petiolate; stipules represented by stipular lines; flowers pentamerous, distylous or homostylous, 1 to many, in axillary or terminal inflorescences; corollas funnelform, the lobes imbricated in bud, bright yellow or orange-yellow; stamens five, epipetalous; style quadrifid at apex; ovary two-locular; fruit a capsule; seeds flattened, usually winged; $n = 8$.

KEY TO THE SPECIES

1. Flowers 2.0–3.5 cm. long, borne in inflorescences of 1–8 flowers; capsules not inflated; seeds wingless or with a strongly asymmetrical entire wing. . . . . 2.
   2. Sepals obtuse, deciduous in fruit; upper half of pedicels bracteolate; capsules terminated by a very short inconspicuous beak; seeds with a strongly asymmetrical, essentially unilateral wing; flowers usually strongly scented. . . . . 1. *G. sempervirens*.
   2. Sepals acuminate, persistent in fruit; upper half of pedicels ebracteolate; capsules terminated by a conspicuous beak; seeds lacking wings; flowers usually odorless. . . . . 2. *G. rankinii*.
1. Flowers 1.2–1.7 cm. long, borne in inflorescences of numerous flowers; capsules inflated; seeds surrounded by an inciso-dentate wing. . . . 3. *G. elegans*.

1. **Gelsemium sempervirens** (L.) Jaume Saint-Hilaire, Expos. Fam. Nat. 1: 338. 1805 (Feb.-Apr.).

Bignonia sempervirens L. Sp. Pl. 2: 623. 1753.
Gelsemium nitidum Michx. Fl. Bor. Am. 1: 120. 1803. Holotype: P (photograph! GH).

Gelsemium lucidum Poir. Encycl. Méth. Bot. Suppl. 2: 714. "1811" (3 July 1812). Holotype: P?

Lisianthus sempervirens Mill. ex Steud. Nomencl. (ed. 1) 358. 1821.

Leaves lanceolate to narrowly ovate, the blades 3–7 cm. long, more or less evergreen, the petioles 0.3–0.5 cm. long; flowers 1–8, corolla 2.5–3.5 cm. long, including the lobes 0.8–1.2 cm. long, bright- to orange-yellow, darker in throat, strongly fragrant (rarely odorless); sepals elliptic, obtuse, 3–5 mm. long, mostly deciduous in fruit; pedicels 0.2–1.2 cm. long, usually densely bracteolate throughout; capsules broadly oblong, 1.5–2.5 cm. long, terminated by a very short beak 0.1–0.2 cm. long representing the base of a deciduous style, woody, hard, tardily dehiscent; seeds brownish, 1.2–1.5 cm. long, including an asymmetrical wing to 1.0 cm. long; $n = 8$. Flowers (January) February–April (May) and occasionally again in late summer or early autumn. Fig. 1a–d.

Distribution. Sea level to 6000 feet (in Mexico and Guatemala). Climbing on fences, low bushes, and trees, or prostrate on ground. Pine or deciduous woodlands in damp to very dry soil, southeastern Virginia to Florida to eastern Texas; mountains of Mexico and Guatemala (Fig. 3).

Representative specimens: **United States.** Arkansas. Bradley Co.: Warren, *Demaree 14364* (GH, NY), *Demaree 14387* (NY). Calhoun Co.: Hampton, *Demaree 14407* (NY). Cleveland Co.: Rye, *Demaree 13568* (NY). Faulkner Co.: Near Republican, *Demaree* in May 1925 (A); near Holland, *Palmer 26534* (A). Hot Springs Co.: Malvern, *Demaree 14493* (GH, NY). Miller Co.: 14 miles east of Texarkana, *Harrison* in 1946 (GH). Monroe Co.: Little Rock, *Manning 85* (GH). Pulaski Co.: Near Ledwidge, *Demaree 8890* (A, NY). Florida. Desoto Co.: 6 miles north of Arcadia, *Ward & Ward 2825* (FLA). Hernando Co.: Brooksville, *Jones* in 1919 (A); Brooksville, *Jones* in 1920 (NY, US). Highland Co.: Sebring, *Hunnewell 9029* (GH). Hillsborough Co.: No definite locality, *Fredholm 6245* (GH). Manatee Co.: Manatee, *Simpson* in 1898 (US); vicinity of Manatee, *Simpson 5* (US). Orange Co.: No definite locality, *Smith* in 1886 (MICH). Pasco Co.: Ehren, *Riegler* in 1961 (FLA); no definite locality, *Barnhart 2518* (NY). Pinellas Co.: No definite locality, *Frank* in 1900 (NY). Polk Co.: Near Lake Marion, *McFarlin 4505* (MICH); Bartow, *McFarlin 6637* (MICH). Sarasota Co.: Sarasota, *Perkins* in 1943 (GH). Tennessee. Hamilton Co.: 3 miles from Sole Creek, *Prather 284* (NY). No definite locality, *Leonard 4133* (US). Texas. Angelina Co.: 4 miles northwest of Jasper, *Cory 52589* (GH, NY); 7 miles southwest of Lufkin, *Cory 49746* (GH, NY, UC, US). Hardin Co.: Southwest of Hooks Switch, *Cory 52693* (NY); Saratoga, *Bailey 941* (US); north of Sour Lake, *Lundell & Lundell 10882* (UC, US). Harris Co.: Houston, *Fisher 14* (US), *Hall 512* (GH, NY, US). Montgomery Co.: Near Conroe, *Palmer 33330* (A). Nacogdoches Co.: 5 miles south of Nacogdoches, *Lundell & Lundell 9761* (MICH, US). Newton Co.: 22 miles south of Newton, *Cory 10914* (GH). Polk Co.: Indian Reservation, *Girvin* on Jan. 31, 1940 (GH, UC); Livingston, *Palmer 5192* (A, MICH, US), *Palmer 6795* (A, US); near Rye, *Traverse 300* (GH). San Jacinto Co.: Without definite locality, *Tharp* in 1935 (MICH, US). Shelby Co.: Five miles north of Center, *Rowell, York & Tharp 47243* (DUKE, GH, NY, UC, US). Tyler Co.: Hyatt Bog, 16 miles south of Woodville, *Cory 52710* (GH, NY). Walker Co.: Near Huntsville, *Tharp* in 1946 (DUKE, NY, UC). Virginia. Greens-

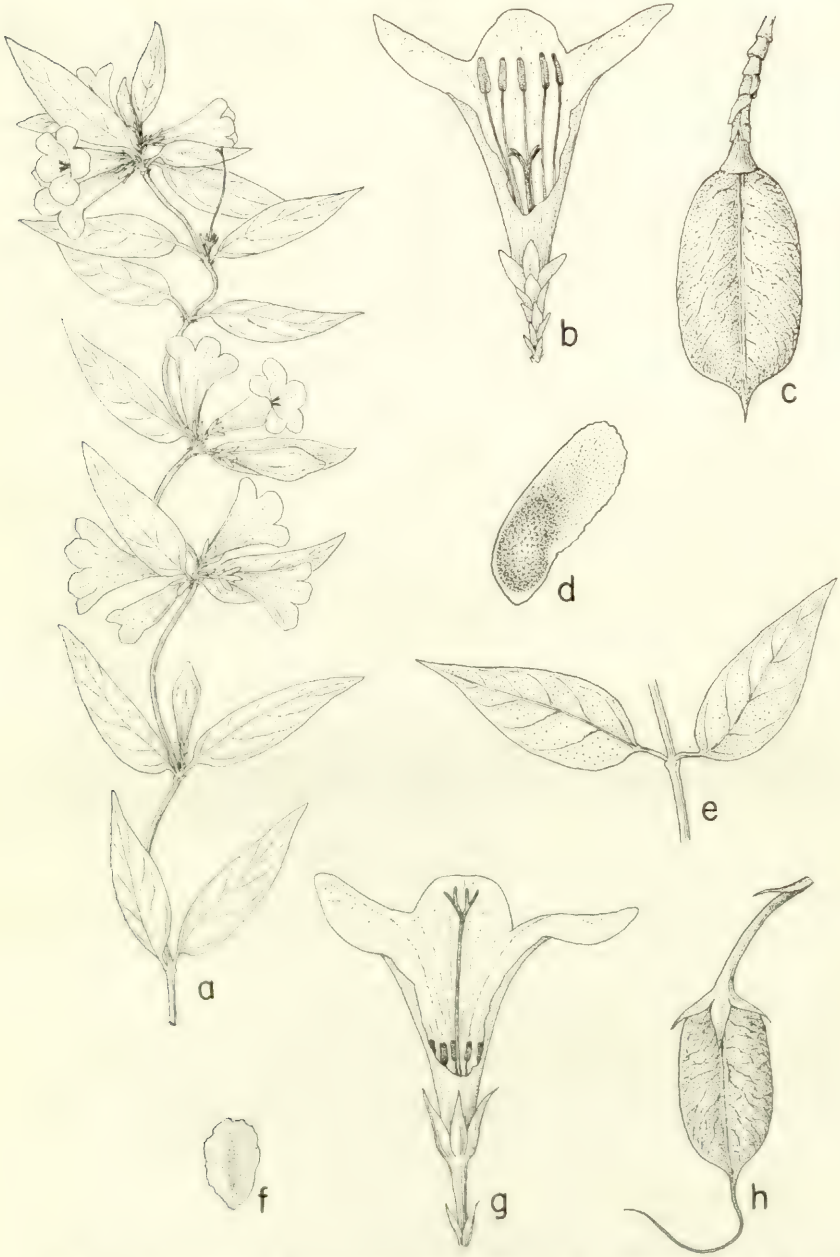

FIG. 1. Characters of *Gelsemium sempervirens* and *G. rankinii*. a–d, *G. sempervirens*. a, habit of flowering stem, × 0.5; b, partly dissected short-styled flower. × 1.5; c, capsule prior to dehiscence, × 2; d, seed, × 3; e–h, *G. rankinii*. e, portion of stem showing rounded leaf-bases often found in the species, × 0.5; f, seed, × 3; g, partly dissected long-styled flower, × 1.5; h, capsule prior to dehiscence, × 2.

ville Co.: Skipper's, *Fernald & Long 7143* (GH). Isle of Wight Co.: South of Lee's Mill, *Fernald, Long & Abbe 14224* (GH); south of Zuni, *Fernald & Mooré 15146* (GH, NY, US). James City Co.: Hampton, *Miller* in 1903 (US); 5 miles west of Toano, *Baldwin 101* (GH); southwest of Williamsburg, *Grimes 2565* (NY); near Williamsburg, *Maxon 10614* (BM, MICH, US). Nansemond Co.: Near Crismond, *Fernald & Long 7142* (GH, US); edge of Dismal Swamp, *Gleason 8617* (NY). Northampton Co.: Savage Neck, *Fernald, Long & Fogg 5411* (GH). Princess Anne Co.: Cape Henry, *Egler 40–180* (NY); Dismal Swamp, *Coville & Kearney 101* (US), *Morong* in 1877 (NY), *Seaman* s.n. (NY, US), *Ward* in 1877 (US); vicinity of Norfolk, *Jensen* in 1907 (A, US); Virginia Beach, *Bartram* in 1908 (GH), *Hollick & Britton* in 1890 (NY, US), *Britton* in 1892 (NY); south of Virginia Beach, *Britton & Small* in 1893 (NY); near Virginia Beach, *Coville & Kearney 17* (US); Virginia Beach, *Fernald & Griscom 2876* (GH), *Stevens* in 1894 (US); without definite locality, *Kearney 1168* (A, US). Southampton Co.: Meherrin River, *Fernald & Long 7141* (GH, NY). Surry Co.: West of Bacon's Castle, *Fernald & Long 7950* (GH). Sussex Co.: Near Moore's Mill, *Fernald & Long 7140* (BM, GH); Spring Grove, *Eaton* in 1938 (GH); northeast of Sussex Courthouse, *Fernald, Long & Abbe 14223* (GH, NY, US). **Guatemala.** ALTA VERAPAZ: Coban, *von Türckheim 881* (GH, K, NY, US), *von Türckheim 1648* (GH, NY, US). ZACAPA: Slopes of Monte Virgen, *Steyermark 42625* (US); between Loma El Picacho and Cerro de Monos, *Steyermark 42773* (A, NY, US). **Mexico.** CHIAPAS: Lagunas de Monte Bello, *Rzedowski 697* (MICH); Pueblo Nuevo Solistahuacán, *Breedlove 9005* (DS, UC). HIDALGO: About 4 miles from Zacualtipán, *Moore 2337* (GH, UC). OAXACA: Talea, *Galeotti 1605* (US). PUEBLA: Zacatlán, *Salazar* on Apr. 3, 1913 (US). VERA CRUZ: Jalapa, *Halsted* s.n. (NY), *Pringle 7766* (GH, MICH, UC), *Smith 1876* (NY, UC); Orizaba, *Botteri 934*, s.d. (BM, K).

In his protologue dealing with this species, Linnaeus (1753) does not cite any specimens except one in Van Royen's herbarium; all other citations are of illustrations and written descriptions. Van Royen's specimen at Leiden lacks flowers and fruits and is, therefore, not unequivocally referable to *G. sempervirens* rather than to *G. rankinii*. Since Linnaeus described fruits, he obviously had more in mind than Van Royen's material alone.

It is quite clear that the Linnaean protologue describes what we now call *Gelsemium sempervirens*. Furthermore, there is no evidence that *G. rankinii* had been collected before the early 19th century, whereas *G. sempervirens* was well known as a cultivated ornamental in Europe as early as the mid-17th century. Although the Van Royen specimen most likely is *G. sempervirens*, I am reluctant to designate it as a lectotype since vegetatively *G. sempervirens* and *G. rankinii* are not easily distinguishable (see Duncan & DeJong, 1964).

The Catesby illustration (1731) is too generalized to be referable to one of these species, but his written description (mentioning fragrance, winged seeds, and geographical distribution) clearly indicates that he was illustrating and describing *G. sempervirens*. So far as I can determine no herbarium material of this species known to have been seen by Catesby exists (see Dandy, 1958), and Catesby himself indicates that he drew largely from nature. Ray's *Historia Plantarum* has a description also

mentioning odor and winged seeds, but there is no indication that a specimen (or illustration) exists. The Plukenet drawing (1696) is very crude, although the winged seeds indicate that he was illustrating *G. sempervirens*. I am designating the illustration by Plukenet as the lectotype of *G. sempervirens* since it is supported by a specimen in the Sloane Herbarium (H.S. 90: 55) at the British Museum which was probably collected by Banister.

I consider *G. nitidum* to be a synonym of *G. sempervirens*. In the Michaux Herbarium at the Muséum National d'Histoire Naturelle in Paris there are three sheets of *Gelsemium* that bear specimens which were presumably collected by Michaux. Two of these sheets bear specimens of *G. rankinii* and the third has *G. sempervirens*. The only sheet annotated as *G. nitidum* is one of those with specimens of *G. rankinii*. Although Michaux had a mixed collection available when he described *G. nitidum*, his characterization of the flower odor indicates that he had *G. sempervirens* in mind. For this reason I do not believe that *G. nitidum* can be considered as the earliest correct name for *G. rankinii* and would suggest that there are good grounds for considering *G. nitidum* as a *nomen confusum*.

2. **Gelsemium rankinii** Small, Addisonia 13: 37. 1928. "Swamps of the Waccamaw River near Hallsboro, North Carolina, collected by *H. A. Rankin*, April 17, 1928." Holotype: NY!

Gelsemium sempervirens (var.) *inodorum* Nutt. Gen. N. Am. Pl. 171. 1818. Holotype: BM! Collected near Savannah, Georgia.

Leaves lanceolate to narrowly ovate, the blades 3.0–7.5 cm. long, more or less evergreen, the petioles 0.3–0.6 cm. long; flowers 1–8; corolla 2.0–3.5 cm. long, the lobes 0.8–1.5 cm. long, bright- to orange-yellow, darker in throat, usually odorless; sepals lanceolate, acuminate, 3–6 mm. long, persistent in fruit; pedicels 0.2–1.0 cm. long, ebracteolate on upper half; capsules oblong, 1.0–1.6 cm. long, terminated by a persistent stylar beak 0.2 cm. long, woody, hard, tardily dehiscent; seeds brownish, 3–4 mm. long, wingless; $n = 8$. Flowering (February) March to April and rarely again in early autumn. FIG. 1e–h.

DISTRIBUTION. At low elevations, climbing on fences, low bushes, and trees, or prostrate on ground. Wet woodlands or swamps of the coastal plains of North Carolina (rare), southern Georgia, northern Florida, southern Mississippi, and southeastern Louisiana (FIG. 3).

Specimens examined: ALABAMA. Escambia Co.: Atmore, *Blanton 206a* (MICH). Mobile Co.: Citronelle, *Milligan* in 1903 (US). FLORIDA. Bay Co.: Between Southport and Westbay, *Hume* in 1930 (NY). Calhoun Co.: Apalachicola, *Mohr & Sargent* in 1898 (US), *Parker* s.n. (NY); near Apalachicola, *Chapman herbarium 474a* (A, GH, NY); Chipola River, east of Clarksville, *Godfrey 56344* (FLA, GH). Escambia Co.: Escambia River near Pensacola, *Sheppard* in 1932 (NY). Franklin Co.: Apalachicola River, *Godfrey & Redfearn 55343* (FLA,

GH, NY); Crooked River, north of Carrabelle, *Godfrey 61749* (FLA). Holmes Co.: Between Chapley and Bonifay, *Godfrey 56366* (DUKE, FLA, GH, NY, UC, US); west of Millers Crossroads, *Godfrey 56403* (FLA, GH). Jackson Co.: West of Cottondale, *Godfrey 56362* (FLA, GH, UC). Leon Co.: West of Tallahassee, *Godfrey 58780* (FLA). Liberty Co.: 6 miles south of Telogia, *Godfrey 59373* (FLA, GH); southeast of Telogia, *Godfrey 61752* (FLA). Wakulla Co.: West of Crawfordville, *Godfrey 58229* (FLA, GH); north of Crawfordville, *Godfrey 59372* (FLA, GH, NY, UC); 30 miles southwest of Tallahassee, *Clewell & Hebb 586* (FLA). Walton Co.: Near Cluster Springs, *Godfrey & Harrison 55399* (FLA, GH, UC, NY); south of De Funiak Springs, *Godfrey 58256* (FLA, GH, NY), *Godfrey 59020* (FLA). GEORGIA. Pierce Co.: Without definite locality, *Godfrey 63251* (FLA). LOUISIANA. St. Martin Parish: St. Martinville, *Langlois* in 1886 (US). St. Tammany Parish: Slidell, *Lemaire 675* (FLA). Tangipahoa Parish: Hammond, *Wilson 346* (FLA); east of Hammond, *Innes & Warnock 722* (GH). Washington Parish: Northeast of Pine, *Correll 9231* (GH). MISSISSIPPI. Jackson Co.: Biloxi, *Tracy 6754* (GH, K); north of Escatawpa, *McDaniel 4055* (FLA). Pearl River Co.: West of Picayune, *Sargent 7943* (FLA). Stone Co.: East of Wiggins, *Kral 16520* (FLA). NORTH CAROLINA. Cumberland Co.: Fayetteville, perhaps cultivated, *Rankin* in 1930 (FLA).

Although the existence of an odorless *Gelsemium* was recognized early in the 19th century, *G. rankinii* was not fully described until 1928. In 1927, H. A. Rankin, a nurseryman in Hallsboro, North Carolina, sent the first of a series of collections of living material of *G. rankinii* to J. K. Small at the New York Botanical Garden. Rankin had noted, among other things, that this "Waccamaw river variety of *Gelsemium*" differed from *G. sempervirens* in its inodorous flowers, later flowering season, and preference for a wetter habitat. Small noted additional differences between these two species in the distribution of bracteoles on the pedicels, shape of the sepals, size and shape of the capsule, and seed characters. Small, in general, accurately characterized *G. rankinii* in his original description of this distinctive species, but perhaps because of the attenuated description and slightly inaccurate key (the leaf-base and anther characters he cites as distinguishing *G. rankinii* and *G. sempervirens* are unreliable) in his *Manual of the Southeastern Flora* (1933), few subsequent workers in the southeastern flora have recognized two species in the region. The majority of collections of *G. rankinii* in herbaria initially have been identified as *G. sempervirens*, but in the late 1950's R. K. Godfrey accurately distinguished between these two species in his herbarium annotations and extensive field collections. Later, Duncan and DeJong (1964) discussed the morphological, ecological, and phenological differences between the two. Because of its occurrence in very wet sites and the ease with which it is confused with the often sympatric *G. sempervirens*, it is probable that *G. rankinii* is more common in the field than might be indicated by its relatively low representation in herbaria.

3. **Gelsemium elegans** (Gardn. & Champ.) Benth. Jour. Linn. Soc. 1: 90. 1857.

Medicia elegans Gardn. & Champ., Hook. Jour. Bot. 1: 324. 1849. Holotype: K!

959 *Leptopteris sumatrana* Blume, Mus. Bot. Lugd. Bat. 1: 240. 1849.
960 *Gelsemium sumatranum* Boerl. Handl. 2: 448. 1899.

Vine to 3.5 m. tall; leaves elliptic to ovate, the blades 6–13 cm. long, sometimes cuspidate, evergreen, the petioles 0.5–1.2 cm. long; flowers numerous, inflorescence terminal or axillary; corolla 1.2–1.7 cm. long including the lobes 0.3–0.8 cm. long, bright- to orange-yellow, odorless (or rarely malodorous?); sepals lanceolate, acuminate, 3–4 mm. long; pedicels 0.3–1.0 cm. long, ebracteolate or with a single subtending bracteole; capsules ovate-elliptic in outline, 0.8–1.5 cm. long, inflated; seeds brownish, 3–4 mm. in diameter, including an inciso-dentate wing ca. 1–2 mm. wide; $n = 8$. Flowering September to December and occasionally at other times. In fruit March and April. FIG. 2a–f.

DISTRIBUTION. Sea level to 6000 feet. Climbing on shrubs and trees in scrub and open woodlands. Assam, northern Burma, northern Thailand, Laos, Viet Nam, southern and southeastern China, Sumatra, and northern Borneo. FIG. 3.

Specimens examined: **Borneo.** BRITISH NORTH BORNEO: From A. B. C. Francis, resident of the interior, *Gibbs 3130* (BM, US). **Burma.** Hkinlum, *Kingdon-Ward 21632* (A, BM); Kachin Hills, *Kingdon-Ward 9020* (A); Hookum Valley to Ava, *Hb. Griffith 3732* (K); Myitkina district, *Lace 6041* (K); Pangyang, Manglon State, *Dickason 9789* (A); Sumpra Bum, *Kingdon-Ward 20566* (A, BM); Wa States, *Maung Po Khant 15216* (K). **China.** FUKIEN: Foochow, *Warburg 5780* (A); Inghok, *Chung 3219* (UC). HAINAN: Dung Ka to Wen Fa Shi, *Chun & Tso 43755* (A, NY, UC); without definite locality, *Liang 64088* (K, NY), *Liang 64203* (NY), *Tang 450* (A), *Wang 35189* (NY, US), *Wang 36650* (A, NY). KWANGSI: Pin-lam, *Ko 55585* (A); Po Yam Shan, *Tsang 22925* (A); Shap Man Taai Shan, *Tsang 22029* (A, BM), *Tsang 24597* (A, NY); Tou Ngok Shan, *Tsang 23174* (A); Tung Loo, *Ching 5645* (A, UC, US); Tsin Hung Shan, *Ching 6860* (A, NY, UC, US); Yao Shan, *Wang 40048* (A); without definite locality, *Chen 91254* (A). KWANGTUNG: Au Tsai, *McClure 3534* (NY); Chung Tung, Tai Tsan, Ying Tak, *Tsang & Wong 3188* (UC); Kwai Shan, *Tsang 28553* (A); Lin Fa Shan, *Tsang 25748* (A); Lofan Mts., *Ford* s.n. (NY); Lofoushan, east river region, *Ho 60162* (NY); Lofoushan Mts., *Tsiang 1777* (A); Naam Kwan Shan, *Tsang 20260* (K, NY); Nam Shan, *Tsang 28874* (A); Ngong T'in Lo Shan, *Taam 347* (A); Shaan Sam village, *McClure 13291* (UC); Sha Lo Shan, *Taam 198* (A); Sinnei district, *T. Ying 2705* (K); Tung Koo Shan, *Tsang 21607* (K, NY, UC); Wan Tong Shan, Tai Tsan Ying Tak, *Tsang & Wong 2703* (UC); Wat Shui Shan, *Wang & Ling 7425* (UC); Weishang, Sunyi, *Tsiang 2705* (NY); Wong Chuk I and vicinity, *Lau 2173* (A); Wu Kan Tin, *Tsiang Ying 83* (A, UC); Wui Shui, *Tang & Fung 31* (NY); Yang Shan and vicinity, *Tsui 693* (K, NY, UC, US); Yun-fou, *Wang 354* (A, UC, US); Yung-Yun city and vicinity, *Lau 799* (A, NY), *Lau 915* (A, NY). YUNNAN: Fo Hai, *Wang 76247* (A), *Wang 77396* (A); Hsian-meng-young, *Wang 80994* (A); Keng-Ma, *Wang 72863* (A); Meng-soong, Dah-meng-lung, Che-li Hsien, *Wang 77992* (A); Mengtz, *Hancock 243* (K); Meng-tsze, *Henry 10452* (A, K, NY, US); Mar-li-po, Sze-tai-po, *Feng 13954* (A); Mar-li-po, Tung-ting, *Feng 13457* (A); Ping-pien Hsien, *Tsai 55136* (A), *Tsai 61880* (A); Si-chour-hsien. Faa-doou, *Feng 12118* (A); Si-chour-hsien, Shiang pyng-shan, *Feng 11485* (A); Tsing-pian, *Tsai 52403* (A); without definite locality,

FIG. 2. Characters of *Gelsemium elegans*. a, portion of flowering stem, × 0.5; b, mature capsules, × 2; c, seed, × 5; d, short-homostyle flower, × 2; e, long-styled flower, × 2; f, short-styled flower, × 2.

Forrest 9214 (A). **Hong Kong.** *N. K. Chun 40251* (K); Kow-loon, *Lamont 467* (A); Lan-tao Island, *Lamont 467* (BM); Lo Fan Shan, *Anonymous* in 1883 (GH); New Territory, *Hb. Hongkong 1818* (A); without definite locality, *Wright 609* (GH, K, US). **India.** ASSAM: Jabocka (= Zoboka), Naga hill, *Prain's col-*

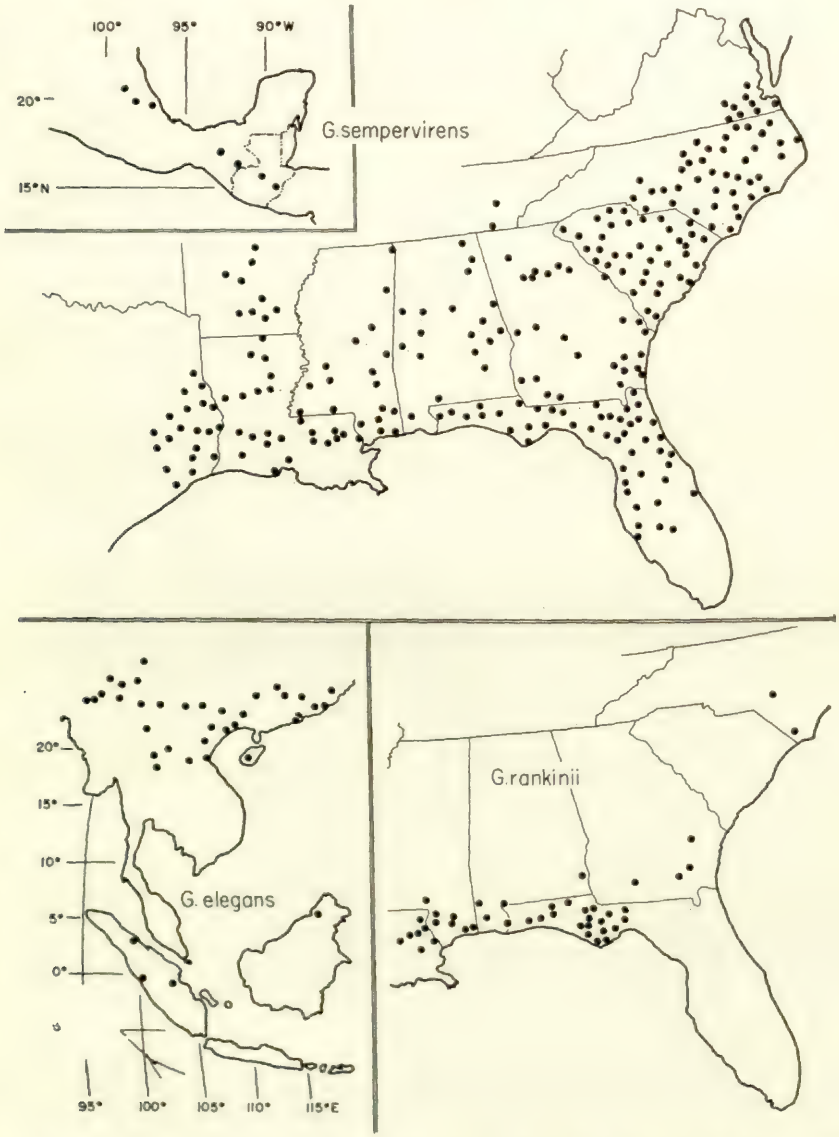

FIG. 3. Distribution of *Gelsemium* species. TOP, distribution of *G. sempervirens* in the southeastern United States and (INSET, upper left) Mexico and Guatemala. LOWER LEFT, distribution of *G. elegans* in southeastern Asia. LOWER RIGHT, distribution of *G. rankinii* in southeastern United States.

lector 959 (A); Lushai Hills, *Parry 322* (K). **Indonesia.** SUMATRA: Maranti, *Rahmat Si Boeea 6116* (A); Mt. Singalan, *Beccari 7* (K), *Beccari 355* (BM). **Laos.** Muang Huang, Wiengchan, *Kerr 20816* (K), *Kerr 200116* (BM). **Thailand.** Pu Huat (Nan), *Kerr 4996* (BM, K). **Viet Nam.** ANNAM: Thanhhoa, *Poilane 1893* (A). TONKIN: Hoa Binh, *Petelot 1906* (NY, US); Kau Nga Shan, *Tsang 30578* (A, K); Kun-Me-Tawng-Mê-Ping, *Garrett 1258* (K); Ouonbi, *Anonymous* in 1885 (A); Taai Wong Mo Shan, *Tsang 27326* (A, K), *Tsang 29611* (A, K).

BREEDING SYSTEM

Gelsemium sempervirens and *G. rankinii* are exclusively distylous, but *G. elegans* has both distylous and homostylous races. The distylous condition in the genus seems first to have been observed by Walter (1788), although it was overlooked by a number of subsequent workers (see Gray, 1873). Distyly in *Gelsemium* is characterized by the occurrence of two types of plants in populations of each species. Some individuals have long-styled flowers, short stamens, and small pollen; others, have short-styled flowers, long stamens, and larger pollen grains (TABLE 4). These two forms also differ in their compatibility relationships (TABLE 2).

TABLE 2. **Results of interspecific and intraspecific pollinations in Gelsemium**

CROSS	NUMBER OF FLOWERS USED	NUMBER OF SEEDS PRODUCED	PER CAPSULE AVERAGE NUMBER OF SEEDS
Interspecific pollinations:			
G. rankinii × *G. sempervirens*	25	5	0.2
G. sempervirens × *G. rankinii*	18	86	4.8
Intraspecific pollinations:			
G. SEMPERVIRENS:			
long selfed, or × long	99	73	0.7
short selfed, or × short	40	53	1.3
AVERAGE			0.9
long × short	58	765	13.2
short × long	28	307	11.2
AVERAGE			12.4
G. RANKINII			
long selfed, or × long	12	0	0.0
short selfed, or × short	25	56	2.2
AVERAGE			1.5
long × short	11	157	14.3
short × long	14	369	26.4
AVERAGE			21.0

The breeding system of *Gelsemium rankinii* and *G. sempervirens* was investigated by conducting a series of self-pollinations, pollinations among long-styled plants, and pollinations among short-styled plants (termed "illegitimate pollinations" by Darwin, 1877), as well as pollinations between long- and short-styled plants ("legitimate pollinations"). The results of the illegitimate pollinations (TABLE 2) indicate that a strong incompatibility system is present in both species since such pollinations result in a seed production that is much lower than seed production following legitimate pollinations. The long-styled form of both species seems to exhibit a stronger self-incompatibility than does the short-styled form. Legitimate pollinations produced a high seed set and it is assumed that in nature the reciprocal differences in position of stigmas and anthers of the two forms enhance legitimate pollinations by insects.

The breeding system of the distylous race of *G. elegans* is unknown, but since the morphological differences between the long- and short-styled forms of this species parallel those that exist in the American species, I assume it has an incompatibility system similar to that of its New World relatives. The homostylous race of *G. elegans* is a short-homostyle, i.e., the flowers have the style length of the short-styled form and the anther

TABLE 3. **Population samples of Gelsemium sempervirens showing representation of plants with long- and short-styled flowers**

COLLECTION NUMBER		LOCALITY	NUMBER OF PLANTS WITH LONG-STYLED FLOWERS	NUMBER OF PLANTS WITH SHORT-STYLED FLOWERS
Ornduff	*6376*	Hoke Co., N. Carolina	30	20
	6388	Duplin Co., N. Carolina	24	27
	6389	Duplin Co., N. Carolina	24	21
	6394	Bladen Co., N. Carolina	22	15
	6702	Orangeburg Co., S. Carolina	13	25
	6704	Bamberg Co., S. Carolina	55	56
	6705	Calhoun Co., S. Carolina	15	17
	6707	Richland Co., S. Carolina	61	44
	6708	Wake Co., N. Carolina	30	37
Breedlove	*9005*	Chiapas, Mexico	14	11
		TOTAL	288	273

position and pollen grain size of the long-styled form (FIG. 2d; TABLE 4). The only living plants of *G. elegans* that were available to me belonged to this homostylous race and were self-compatible, as would be expected from the position of the reproductive organs. This occurrence of a short-homostyle race in a normally distylous species is unusual. In the majority of heterostylous species in other plant families (such as Primulaceae, Rubiaceae, and Turneraceae) in which homostylous plants occur, the latter are generally long-homostyles.

Data concerning the pollination biology of *Gelsemium* are scant. Two collections of bees visiting *G. sempervirens* have been made. My collection was made in North Carolina and was identified by T. B. Mitchell. The most common visitors to the flowers were males and females of the large-bodied *Emphoropsis laboriosa* (Fabr.) (Anthophoridae). In addition, smaller-bodied bees belonging to the genera *Dialictus* and *Ceratina* were also collected. In Virginia, Hurd (pers. comm.) has noted *E. laboriosa* as well as the bumblebee *Bombus impatiens* Cresson (Apidae) visiting flowers of *G. sempervirens*. It is probable that the larger-bodied bees are the chief pollinators of *Gelsemium*, since the shape and size of the corolla tube as well as the relative position of anthers and stigmas require relatively large-bodied insects to effect pollen transfer.

Population samples of *G. sempervirens* indicate that long- and short-styled plants are present in a 1:1 ratio (TABLE 3). This is probably also the case for *G. rankinii* (Duncan & DeJong, 1964).

Elsewhere in the Loganiaceae, heterostyly has been reported for *Mostuea* (Leeuwenberg, 1961) and has also been suggested for *Buddleia* (Leenhouts, 1962), although the latter genus requires further study. Otherwise, heterostyly is unknown in this family, although it occurs in the related Oleaceae and Rubiaceae. Despite the rarity of heterostyly in the Loganiaceae and its possibly independent evolutionary origin in this family, the morphological expression of heterostyly in *Gelsemium* is remarkably similar to that which exists in other unrelated distylous genera (Darwin, 1877; Vuilleumier, 1967).

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TABLE 4. **Measurements of style length, stamen length, and pollen size of heterostylous and homostylous Gelsemium flowers**

SPECIES	STYLE LENGTH	SAMPLE SIZE	STYLE LENGTH (with range in cm.)	STAMEN LENGTH (with range in cm.)	POLLEN SIZE (with range in μ; sample size)
G. sempervirens	Long	36	1.8 (1.2–2.3)	0.8 (0.7–0.9)	33.9 (31.5–36.4; 260)
	Short	38	0.8 (0.5–1.3)	1.6 (1.5–2.3)	37.0 (32.8–40.1; 200)
G. rankinii	Long	10	2.2 (1.8–2.4)	0.7 (0.6–0.9)	31.5 (28.1–34.2; 200)
	Short	10	0.7 (0.6–0.8)	1.8 (1.7–2.0)	36.1 (34.2–38.1; 200)
G. elegans	Long	10	1.2 (1.0–1.4)	0.5 (0.4–0.6)	27.7 (22.8–33.2; 180)
	Short	10	0.7 (0.5–0.8)	1.1 (1.0–1.4)	30.8 (25.6–38.0; 180)
	Homostyle	7	0.7 (0.6–0.8)	0.6 (0.5–0.7)	26.7 (24.0–30.8; 60)

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THE GENERA OF ULMACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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ULMACEAE Mirbel, Elém. Phys. Vég. Bot. **2**: 905. 1815, nom. cons.

(ELM FAMILY)

Trees or shrubs with watery sap; leaves with conduplicate vernation, alternate [rarely opposite], simple, the blade usually oblique at base, entire to variously serrate, petiolate; stipules paired, lateral or intrapetiolar, caducous; flowers perfect to imperfect (often by abortion of either androecium or gynoecium), actinomorphic to slightly zygomorphic, solitary, cymose, or in axillary fasciculate aggregations, usually borne on branchlets of the previous season (Ulmeae) or of the current season (Celteae). Perianth herbaceous, subcampanulate, (2–)4–8(–9)-lobed, the lobes free or variously fused, imbricate [valvate], persistent. Stamens erect in bud, hypogynous, arising from the base of the perianth, usually the same number as and opposite the perianth lobes [or sometimes more], the filaments distinct, the anthers bilocular with longitudinal dehiscence, extrorse or introrse; pollen 2–5(–6) aperturate (-porate, -colpate or -rupate), oblate to oblate-spheroidal. Gynoecium composed of 2 connate carpels; styles 2, linear, stigmatose along the upper inner surface, ovary superior, usually 1-loculate (occasionally 2-loculate in *Ulmus*), sessile to stipitate, the ovule 1, anatropous or amphitropous, pendulous from the apex of the locule, with 2 integuments. Fruit a samara, dry or thinly fleshy, often winged or appendaged, the seed with a straight embryo and without endosperm, or fruit a drupe, the seed with a curved embryo with

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his thorough editing and valuable suggestions in the course of this study. Dr. John W. Thieret has kindly read the manuscript and has offered a number of useful and much-appreciated comments. Mrs. Nancy Dunkly has helped greatly in checking the bibliography and in typing the manuscript copy. In the illustration of *Trema*, b, c, and e–i were drawn by the late Dorothy H. Marsh; the remaining items and the illustration of *Ulmus* are by Arnold D. Clapman. The late Dr. G. K. Brizicky supervised the drawings and made the dissections from materials collected by Dr. Wood.

folded or rolled cotyledons and usually with scanty endosperm. Embryo sac of the Polygonum type (*Celtis*) or of the Adoxa and Drusa types (*Ulmus*). Chromosome numbers, $x = 10, 11, 14$. (Celtaceae Link.) TYPE GENUS: *Ulmus L.*

A family of about 15 genera and 150–200 species distributed throughout much of the Northern Hemisphere and reaching into subtropical and tropical areas. Four genera are represented in the continental United States: *Ulmus*, with six species in the southeastern United States; *Celtis*, with five species in our range; *Planera*, a monotypic genus of the southeastern United States; and *Trema*, largely tropical, but with two species reaching into southern and central Florida. Additional New World genera include *Lozanella* Greenman, *Ampelocera* Klotzsch, and *Mirandaceltis* A. J. Sharp, all essentially tropical.

The Ulmaceae, one of five families in the order of Urticales, is distinguished from its nearest new world relatives the Moraceae, Cannabaceae, and Urticaceae by watery sap, leaves usually oblique at the base, flowers usually perfect, stamens erect in bud, fruit a samara or drupe, and seed with little or no endosperm. Using floral morphology and anatomy, Bechtel demonstrated the Ulmaceae to be the most primitive family in the order Urticales. In *Ulmus*, the flowers show evidence of suppression of a whorl of stamens and of one of the perianth whorls. Although the floral parts are cyclic in most ulmaceous genera, those of *Ulmus* are spirally arranged. In the gynoecium of Ulmaceae the many abortive vascular strands suggest suppression of carpels, the bicarpellate condition possibly having been derived from a polycarpellate condition. Tippo, using data from wood anatomy, confirmed this phylogenetic arrangement. It was pointed out that ring porosity appeared more commonly in the Ulmaceae (essentially temperate) than in the Moraceae (essentially tropical).

Dumortier divided the family into tribes Celteae (incorrectly Celtideae) and Ulmeae, but Engler raised the two divisions to subfamilial status. A third subfamily infrequently recognized is Barbeyoideae, but many workers place the monotypic genus *Barbeya* Schweinf. in a family of its own, Barbeyaceae Rendle.

The two tribes (subfamilies) can generally be separated by their pollen, the Ulmeae usually having 4- or 5-porate, -colpate, or -rupate grains, the Celteae usually having 2- or 3-porate grains. The only exception is *Zelkova* (Celteae) which typically has the *Ulmus* type of pollen.

Fairly abundant in the fossil record, fruits, as well as leaves, of *Ulmus* and *Celtis* have been found in large numbers. *Zelkova*, *Hemiptelea*, and *Pteroceltis* also are known as fossils.

The wood of *Ulmus* is of limited importance in the manufacture of furniture. The bark of *U. rubra*, high in mucilage content, has been used in medicinal preparations. Numerous cultivars of *Ulmus*, many resulting from efforts to produce disease resistant forms, are grown domestically as ornamentals.

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Key to the Genera of Ulmaceae

A. Flowers usually perfect; fruits either flattened or ± dry with fleshy protuberances; embryo straight, cotyledons flat or longitudinally folded (Ulmeae).
  B. Fruit a flat, winged samara; leaves usually biserrate; flowers appearing either before or after the leaves. ..... 1. *Ulmus.*
  B. Fruit ovoid, wingless with numerous fleshy protuberances; leaves mostly serrate; flowers appearing with the leaves. ..... 2. *Planera.*

A. Flowers usually imperfect; fruits drupaceous; embryo curved, cotyledons variously folded (Celteae).
  C. Carpellate flowers solitary or in few-flowered fascicles; anthers extrorse; plants often spinose. ..... 3. *Celtis.*
  C. Carpellate flowers in axillary, subsessile cymes; anthers introrse; plants unarmed. ..... 4. *Trema.*

Tribe Ulmeae [Dumort.]

1. **Ulmus** Linnaeus, Sp. Pl. 1: 225. 1753; Gen. Pl. ed. 5. 106. 1754.

Trees (or infrequently shrubs) of various habitats, the bark usually deeply furrowed; branches unarmed, slender, terete, often with corky wings; leaf buds axillary, covered with numerous ovate to rounded chestnut-brown, glabrous to pubescent, closely imbricated scales, the inner scales accrescent and replacing the stipules, deciduous, leaving ring-like scars. Leaves distichous, petiolate, simply or doubly serrate, pinnately veined, deciduous to subpersistent [rarely persisting until new growth]; stipules lateral, linear-lanceolate to obovate, entire, free or connate at the base, scarious, inclosing the leaf in bud, caducous. Flowers perfect [rarely imperfect, the plants then polygamous], vernal to autumnal, minute, articulate on slender 2-bracteolate pedicels, produced in axillary subsessile or pedicellate cymes or racemes. Perianth uniseriate, campanulate, slightly to deeply (4–)5(–9)-lobed, membranaceous, marcescent. Stamens with the filaments filiform to ± flattened, exserted after anthesis; anthers oblong, emarginate, subcordate at the base, dorsified below the middle, extrorse. Style deeply 2-lobed, divergent, the lobes papillate and stigmatic on the inner face, ovary sessile or stipitate, compressed, glabrous or hirsute, usually 1-locular by abortion, rarely 2-locular; ovule amphitropous, micropyle extrorse, superior. Fruit a ± flattened samara, ovate to oblong, often oblique, sessile or stipitate, surrounded at the base by the marcescent calyx, often beaked by the remnants of the persistent styles, occasionally marked vertically by the thickened line of union of the two carpels, and

with a thin reticulate-venulose, membranaceous, light brown, broad or narrow wing [± unwinged], the wing often ciliate on the margin. Seed ovate, compressed, marked on the abaxial edge with the thin raphe, without endosperm; seed coat membranaceous, light or dark brown,

FIG. 1. **Ulmus.** a–h, *U. americana*: a, mature leaf × ½; b, branchlet with flowers, × ½; c, flower at time of shedding of pollen, × 5; d, flower with receptive stigmas, × 5; e, gynoecium in partial section to show ovule, × 5; f, mature fruit, × 1; g, seed, × 4; h, embryo, × 4. i–k, *U. rubra*: i, mature leaf, × ½; j, branchlet with nearly mature fruit and expanding leaves, × ½; k, mature fruit, × 1. l, *U. crassifolia*, leaf, × 1. m, *U. alata*, mature leaf, × ½.

rarely produced into a narrow wing. Embryo straight; cotyledons flat or slightly convex, fleshy, much longer than the superior radicle, the hilum oblong-linear, pale. (Including *Microptelea* Spach, *Chaetoptelea* Liebmann.) TYPE SPECIES: *U. campestris* L. = *U. glabra* Hudson; see

R. Melville, Jour. Bot. 76: 261–265. 1938, and A. Rehder, Bibl. Cult. Trees & Shrubs 135. 1949.[2] (Ancient Latin name for elm.) — ELM.

A genus of 25–30 species widely distributed through temperate and boreal regions of the Northern Hemisphere, with central and northern Asia the apparent center of distribution. Six species occur in eastern North America, but the genus is noticeably absent from western North America. *Ulmus* is found throughout Europe, extends south to the mountains of northern Africa, east to Turkey and the Caucasus Mountains, Pakistan, and the western Himalayas, to Siberia, Manchuria, and northern China to Japan. The genus has been divided into various subgenera, sections, and series (Spach, 1841; Planchon, 1848; Schneider, 1904); in the most recent subgeneric classification, Rehder (1949) recognized five sections, each represented in our range by at least one species.

KEY TO THE SECTIONS OF ULMUS IN THE SOUTHEASTERN UNITED STATES

A. Flowers vernal, appearing before the leaves; perianth with short, often unequal lobes.
  B. Flowers subsessile to very short pedicellate, not pendulous; samaras not ciliate on the margins. ..... Sect. ULMUS.
  B. Flowers long pedicellate, often unequally so, becoming pendulous; samaras marginally ciliate.
    C. Flowers fasciculate, the floral axis only slightly elongating; samaras glabrous on the sides; branches without corky wings. ..... Sect. BLEPHAROCARPUS.
    C. Flowers racemose, the floral axis slender and elongating; samaras pubescent on the sides; branches often with corky wings. ..... Sect. CHAETOPTELEA.
A. Flowers autumnal or appearing considerably after the leaves; perianth with the lobes deeply divided, often to the base.
  D. Flowers fasciculate, not pendulous, 4–5(–8)-merous; leaves subpersistent to ± persistent. ..... Sect. MICROPTELEA.
  D. Flowers in pendulous racemes, 6–9-merous; leaves deciduous. ..... Sect. TRICHOPTELEA.

Section ULMUS (§ *Madocarpus* Dumort.), an extensive Eurasian group, is represented in North America only by *Ulmus rubra* Muhl. (*U. fulva* Michx.), slippery elm, $2n = 28$. Occurring from southwestern Maine westward through southern Ontario to eastern North Dakota, southward to western Oklahoma and central and southeastern Texas, and eastward to central Georgia and northwestern Florida, *U. rubra* is commonly found in lowlands, especially in rich soil along stream banks and on low,

[2] The Linnaean name for the type species of the name *Ulmus* is *U. campestris* L. Since it has been used for three other species (*U. glabra* Hudson, *U. carpinifolia* Ruppius ex Suckow, and *U. procera* R. A. Salisbury) this name is now considered a *nomen ambiguum* to be rejected under Art. 69 of the Code (see Report of Standing Committee on Stabilization, Synop. Prop. Bot. Nomencl. XI Internatl. Bot. Congr., Seattle, 1969. Append. E, p. 113. 1969.). The correct name for this species appears to be *U. glabra* Huds. (cf. Melville, 1938, and Rehder, 1949).

rocky hillsides. In addition to the sectional characters, *U. rubra* is characterized by the ciliate leaves being scabrous above and by the very mucilaginous inner bark. Sterile, scabrous-leaved specimens of *U. americana* may be confused with this species but are distinguishable by the hardly mucilaginous bark.

Section BLEPHAROCARPUS Dumort. comprises a small group of European species and a single North American one, *Ulmus americana* L., American, soft, water, or white elm, $2n = (28)\ 56$. It occupies a broad range from Newfoundland west to southern Manitoba and eastern Saskatchewan, south to North Dakota, southeastern Montana, western Nebraska, western Oklahoma and central Texas, and in the east to Florida. It is readily identified by the flowers borne in close fascicles with elongating, pendulous pedicels, and a marginally ciliate, elliptic samara. The leaves may be smooth to scabrous above.

Fernald recognized four forms based on combinations of two pairs of vegetative characters: f. *pendula* (Ait.) Fern., with pubescent branchlets and the leaves smooth above; f. *laevior* Fern., with the branchlets as well as the upper leaf surfaces smooth; f. *alba* (Ait.) Fern., with pubescent branchlets and the leaves harshly scabrous above; and f. *intercedens* Fern., with glabrous branchlets and the leaves harshly scabrous above. All four can be found in our range, but attempts to distinguish them can end in frustration, for both smooth and scabrous leaves can be found on the same tree (Thieret). Varietas *floridana* (Chapm.) Little (*U. floridana* Chapm.), Florida elm, differing from var. *americana* only in degree in several quantitative characters (cf. Kurz & Godfrey, p. 113) is found on the Coastal Plain from eastern North Carolina to central Florida.

Natural hybrids of *Ulmus americana* are rare. Artificial hybrids have been made between this species and both *U. pumila* L., $2n = 28$, and *U. laevis* Pallas (cited as *U. pedunculata* Fougeroux by Winieski), but seed production from the crosses was very low and germination of the hybrid seeds even lower. Sax (1933) postulated that *U. americana* rarely crosses successfully with other *Ulmus* species because of an inability of the chromosomes to pair, since most species are diploid ($2n = 28$), while most American elms are tetraploids. Much of the genetic research with the elms, especially *U. americana*, has been concerned with the development of various races and hybrids which would hopefully be resistant to the Dutch elm disease and/or phloem necrosis. The closest relative of *U. americana* is the European *U. laevis* Pallas, $2n = 28$.

Section CHAETOPTELEA (Liebm.) Schneid., a New World section of only three species, is represented in our range by *Ulmus Thomasii* Sarg. and *U. alata* Michx., both of which frequently have corky-winged branchlets. *Ulmus Thomasii*, rock elm, $2n = 28$, is known from western Vermont west to southern Ontario, central Michigan, Wisconsin, northern Minnesota, and southeastern South Dakota, south to northern and eastern Nebraska and eastern Kansas, east to Missouri and Tennessee (and locally in northwestern Arkansas), and northeastward to Ohio and New

York. *Ulmas alata*, wahoo, winged, or cork elm, occurs from Virginia to Kentucky, southern Indiana, southern Illinois, and Missouri, south to central Oklahoma, eastern and southeastern Texas, and east to central Florida. Both species are commonly found on dry, rocky uplands, slopes, or cliffs. The two are easily distinguished by the broadly elliptic samaras and larger, distinctly petiolate leaves of *U. Thomasii*, in contrast with the lanceolate-ovate samaras and small, subsessile leaves of *U. alata*. The third member of this section is *U. mexicana* (Liebm.) Planch. (*Chaetoptelea mexicana* Liebm.), which occurs in mountainous areas from southern Mexico southward to Panama.

Section MICROPTELEA (Spach) Benth. & Hook. includes only the closely related but widely separated *Ulmus parvifolia* Jacq., of eastern Asia, and *U. crassifolia* Nutt., cedar, basket, or southern rock elm, of the southern United States. The latter is found in southwestern Tennessee, Arkansas, and southern Oklahoma, south to central and southern Texas, Louisiana, and western Mississippi. An isolated station was recently discovered in northern Florida (Suwanee County), and intervening stations should be looked for in Alabama and eastern Mississippi. It is questionably known from Nuevo León, Mexico. The older branches frequently have corky wings. This species, along with its Asian counterpart, is usually a tall tree reaching to 25 m. and is often free of branches for half its height. The frequently thick bark usually peels off in scales, exposing the brownish inner bark. Although described as a member of the following section, the poorly known *U. monterreyensis* C. H. Muller of Nuevo León, Mexico, is vegetatively very similar to *U. crassifolia*, but fruits and additional flowering material are needed before it can be placed properly.

Section TRICHOPTELEA Schneid. contains *Ulmus serotina* Sarg., September elm, probably the sole member of this section, which ranges from southern Illinois, Kentucky, and Tennessee, south to northern Alabama, northwestern Georgia, Arkansas, and eastern Oklahoma. Flowering and fruiting later than *U. crassifolia*, *U. serotina* is usually found in bottom lands and on limestone hills.

Of the numerous species and cultivars in cultivation (see Green), three appear to be naturalized and spreading from cultivation. The English elm, *Ulmus procera* Salisb. (§ *Ulmus*), naturalized from southern New England and New York southward to Virginia, has been reported by Crutchfield from Roanoke Island, North Carolina. The other European introduction in eastern North America, *U. glabra* Huds. (*U. campestris* L., pro parte) (§ *Ulmus*), Wych elm, has not been reported as being naturalized in our range. The third species, *U. pumila* L., (§ *Ulmus*), dwarf or Siberian elm, introduced from Asia and apparently stabilized from Minnesota to Kansas and in Utah, has also been reported from North Carolina by Crutchfield. This species has been planted in the northeastern and midwestern United States in parks, along boulevards, and on farms for windbreaks. It has mistakenly been called *U.*

parvifolia, Chinese elm, a species of eastern Siberia, northern China, and Japan which is not cultivated to any extent in the United States.

Pollination in *Ulmus* is clearly by wind, and, within our range, the elms contribute to both the early spring hayfever or tree-fever and the late-summer hayfever seasons. *Ulmus alata*, *U. americana*, and possibly *U. rubra*, all producing prodigious amounts of pollen, cause hayfever mainly in February and March in the Virginias and Carolinas (Wodehouse). Flowering about the same time as the ragweeds, *U. crassifolia* usually complicates late summer hayfever. *Ulmus serotina*, does not appear to be significant as a hayfever plant.

Although the flowers of *Ulmus* are perfect, cross pollination is apparently necessary to insure good seed production. It has not been clearly established whether the plants are partially or wholly self-incompatible or whether the proterogyny or proterandry reported in several species accounts for the lack of self fertilization. Further study of the floral maturation patterns is needed.

The base chromosome number for *Ulmus* appears to be 14 ($2n = 28$). Chromosome numbers for at least 13 species have been reported, with most *U. americana* and possibly some *U. glabra* at the tetraploid level, $2n = 56$. According to Sax, *U. americana* is probably an autotetraploid. Ehrenberg, in a study of the pollen of *U. glabra*, reported partial sterility in 47.2 per cent of the plants studied. The embryo sacs are tetrasporic and of the Adoxa or Drusa types or a modified form of the two.

First appearing in the Upper Cretaceous, *Ulmus* became abundant and widespread in the rocks of the early Tertiary (over 28 Eocene species described). Apparently reaching its maximum distribution during the Miocene (ca. 30 species), *Ulmus* was widespread in Europe, both eastern and western North America, and Asia. Pleistocene deposits have yielded some eight species, most of which are still extant.

Although many species of elms have corky flanges (wings) on the branches, the nature of these has been studied only in *U.* × *hollandica* Mill. in which the wings are produced by a symmetrical longitudinal splitting of the cork into bands which project like wings from the stem surface (Smithson). The corky wings found in *U. alata* and *U. crassifolia* have not been investigated.

Of the many diseases of elms, none has received as much attention as the Dutch elm disease, so called because much of the early work on it was done in Holland. Discovered in France in 1918 and now occurring over most of western Europe, it reached the United States about 1930, probably in a shipment of elm burl logs imported for veneer. It has now spread throughout the northeastern United States and has reached Ontario and Quebec and at least as far west as Illinois and as far south as Tennessee. *Ulmus* species vary in susceptibility, but *U. americana*, widely planted as a street tree in northeastern North America, is especially vulnerable and is possibly threatened with extinction. The disease is caused by an ascomycete, *Ceratocystis ulmi* (*Ceratostomella ulmi*), a yeast-like stage of which spreads through the vessels. It both produces

a toxin and stimulates the production of tyloses in the vessels, blocking water flow and causing wilting and death of the infected parts. The fungal spores are carried by the bark beetles *Scolytus multistriatus* and *Hylurgopinus rufipes* (and perhaps others), which lay their eggs in dead or injured bark of the trunk and branches of elms. The larvae tunnel under the bark in a characteristic feather-like pattern. The fungus sporulates in cracks in the bark, beneath dying bark, and in the beetle tunnels, and the sticky spores are carried by the emerging adult beetles to uninfected branches of the same or other trees where the beetles feed for a time before breeding. The spores enter the healthy tissues through the feeding wounds made by the beetles in the thin bark of young shoots. No satisfactory control has yet been found, but control of the beetles through spraying and removal and burning of diseased trees is widely practiced in cities. Several clones have been reported to be resistant to the disease: a highly regarded one is *U. carpinifolia* 'Christine Buisman', which, although showing considerable resistance to phloem necrosis as well, is unusually susceptible to a dieback caused by *Nectria cinnabarina*.

Phloem necrosis, caused by the virus *Morsus ulmi*, is even more deadly and has been known to kill an elm in a single season. The virus attacks the phloem, eventually destroying the phloem elements, interrupting the food supply to the roots, and causing in the more advanced stages small and even large roots to die. It is transmitted by the elm leaf-hopper, *Scaphiodeus luteolus*, which can be controlled by various insecticides. An American disease, cephalosporium wilt, caused by the imperfect fungus *Dothiorella ulmi*, causes foliage wilting and dieback of the young branches. Judicious pruning can usually control and eradicate this threat.

Elms are attacked by numerous insect pests, including the elm leaf-curl aphid, *Ariosoma ulmi*; the leaf beetle, *Galerucella luteola*; the elm borer, *Saperda tridentata*; the elm lace bug, *Corythucha ulmi*; and the gypsy moth, *Porthetria dispar*.

The wood of elm is heavy, tough, strong, often flexible, durable under water, often difficult to split, and fairly attractive in appearance. The sapwood is usually yellowish or cream colored with brown or grayish-brown heartwood. The wood of all the species in our range is ring porous. A minor lumber source, elm wood is used in shipbuilding, panelling, crates, and in some furniture. At one time it was commonly used for wheel hubs. High in mucilage content, the inner bark of *U. rubra*, and to a lesser extent that of *U. americana*, has been used in various decoctions in folk and Indian medicine in the southeastern United States.

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Many popular or semipopular articles about *Ulmus* and numerous references concerning the Dutch elm disease have been omitted. Under family references see Baillon, 187; Bernard, 1108–1112; Berry, 146–153; Fowells, 724–742; Gibson, 379–394; Jongmans, 23–66; Kurz & Godfrey, 109–115; Vines, 208–214; West & Arnold, 58–60.

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2. **Planera** J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2: 150. 1791.

Deciduous trees or large shrubs of wet habitats, usually less than 20 m. tall, with scaly bark, the inner bark reddish brown; branchlets slender, terete, unarmed, puberulous; lenticels pale, scattered; leaf scars small, ± orbicular; buds axillary, minute, subglobose, covered with thin, closely imbricate scales. Leaves petiolate, ovate-oblong, coarsely serrate, acute to rounded at apex, oblique to rounded at base, pinnately veined, the veins ± conspicuously anastomosing beneath; stipules free, lateral, ovate, caducous. Plants polygamous, flowers perfect or often functionally imperfect, fasciculate at the nodes of the one-year-old branches, articulate, short-pedicellate, the pedicels ebracteolate, the lower flowers often staminate. Perianth campanulate, 4- or 5-lobed from midway to near the base, the lobes rounded apically, greenish yellow, subscarious, submarcescent. Stamens as many as the perianth lobes in staminate flowers, in carpellate flowers often reduced or wanting; filaments filiform, exserted; anthers introrse, ovate, emarginate apically, cordate basally, dorsifixed below the middle; pollen 4–5-porate, -colpate or -rupate. Gynoecium often rudimentary in staminate flowers; styles 2, elongate, papillo-stigmatic on the inner faces, united at the base, wanting in staminate flowers; ovary ovate, stipitate, tuberculate, 1-loculate, the ovule anatropous to shortly amphitropous. Fruit obliquely ovate to oblong, ± compressed, keeled on the back, with numerous fleshy protuberances, often inclosed basally by the marcescent calyx, often beaked by the persistent style. Seeds plano-compressed, ovoid, often oblique, testa membranaceous, endosperm absent. Embryo straight; cotyledons ± thick, flat, slightly unequal, the apex of the larger hooded and slightly infolding the smaller, the radicle minute, directed toward the linear hilum. TYPE SPECIES: *P. aquatica* J. F. Gmelin (*Anonymos aquatica* Walt., nom. invalid., cf. ICBN 1966. Art. 20, 43.) (Named for the German botanist Johann Jakob Planer, 1743–1789.) — WATER ELM, PLANER TREE.

A monotypic genus of the southeastern United States ranging along the Coastal Plain from southeastern North Carolina south to northern Florida, west to eastern Texas, and north in the Mississippi Embayment to southeastern Oklahoma, southeastern Missouri, southern Illinois, western Kentucky, and western Tennessee. *Planera aquatica* appears to be restricted to swamps, margins of sluggish streams or rivers and alluvial flood plains. It is frequently found growing in permanent water up to a meter deep, but can withstand long periods of inundation at greater depths (McAtee).

Flowering begins in February and continues into April, with the fruits maturing approximately one month following anthesis. The seed viability has been reported to be very high (McAtee). The seeds are a major food source for waterfowl, especially mallard ducks. A study conducted in Louisiana from October through December on 171 mallard ducks revealed that 45.5 per cent of their total subsistence consisted of seeds of

P. aquatica (McAtee). Other species of ducks occasionally feed upon the seeds, but not as a major food supply (McAtee, Mabbott). The seeds apparently remain viable in standing water, thus supplying waterfowl with an overwintering food.

Several species of *Planera* have been described on the basis of fossil leaves and leaf fragments. *Planera longifolia* and *P. Ungeri* are attributed to the Upper and Middle Miocene in the central Rocky Mountain area (Lesquereux, 1878, 1883), and *P. Ungeri* has been reported by Heer from Alaska. Berry (1924) considered the genus to be an old one, with four Upper Cretaceous species distributed from western Greenland to North Carolina. Also three or four Eocene species are known only from North America and the Arctic localities. *Planera* is also represented in the Miocene of Europe and North America and in the Pliocene of Europe and Asia.

The wood of *Planera* is considered to be of little or no use economically. In comparison with the wood of *Ulmus*, Gibson found that of *Planera* to be lighter in weight (specific gravity 0.53), poorer in fuel value, weaker, and more brittle. The wood is described as being soft, light brown in color with almost white sapwood. *Planera* differs from *Ulmus* in that the annual rings lack the rows of large open vessel-pores common in *Ulmus*.

The genus is closely related to *Ulmus* but has partially imperfect flowers and a characteristic wingless fruit with irregular fleshy protuberances. Unfortunately little is known of the genus in regard to its overall biology, i.e., floral anatomy, embryology, cytology, and ecology.

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Under family references see also BERRY (1924, pp. 158, 159), GIBSON (pp. 397–399), JONGMANS (pp. 16–18), KURZ & GODFREY (pp. 107, 108), LESQUEREUX (1883, p. 161; 1878, p. 189), HEER (p. 34), PRIEMER (pp. 453, 454), and WEST & ARNOLD (p. 56).

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Tribe CELTEAE Dumort., "Celtideae"

3. **Celtis** Linnaeus, Sp. Pl. 2: 1043. 1753; Gen. Pl. ed. 5. 467. 1754.

Small to moderate-sized or large trees or shrubs of variable habitats, the bark smooth or often fissured and conspicuously warty; branches un-

armed or spinose; buds scaly or naked. Leaves distichous, serrate or entire, often oblique at the base, pinnately 3(–5)-veined, petiolate, membranaceous to coriaceous, deciduous [or persistent]; stipules lateral, free, usually scarious, caducous. Plants monoecious or rarely polygamomonoecious, the flowers vernal, small, pedicellate on the branches of the year, usually functionally imperfect, rarely functionally perfect, the usually lower staminate flowers cymose or fascicled, the carpellate flowers solitary or in few-flowered fascicles from the axils of the upper leaves. Perianth imbricate, slightly to deeply 4(5)-lobed, the lobes deciduous. Stamens as many as the perianth lobes, inserted on the usually densely pilose receptacle; filaments subulate, sometimes incurved in bud and spreading elastically, exserted after anthesis; in carpellate flowers usually shorter and included and often nonfunctional, rarely wanting; anthers ovate, dorsifixed just above the emarginate base, close together and face to face in bud, extrorse. Gynoecium in staminate flowers minute and rudimentary; in carpellate flowers style short, sessile, divided into two divergent, elongate, reflexed lobes, the lobes entire or bifid, papillate-stigmatic on the inner face, deciduous; ovary ovate, sessile, 1-loculate; ovule anatropous, with two integuments. Fruit a fleshy drupe, ovoid or globose, the outer part of mesocarp thick and firm, the inner thin and fleshy, the stone thick-walled, bony, smooth or rugose. Seed filling the locule; endosperm scanty, gelatinous, nearly inclosed between the folds of the cotyledons, or wanting; seed coat membranaceous, the chalaza colored, close to the minute hilum. Embryo curved; cotyledons broad, foliaceous, conduplicate or rarely flat, variously folded, corrugate, incumbent on or embracing the short superior radicle. (*Mertensia* HBK. non L., *Momisia* F. G. Dietr., *Solenostigma* Endl.). TYPE SPECIES: *C. australis* L., of Europe and Asia. (Name the classical Latin one given by Pliny for an African lotus with sweet berries, possibly *Celtis australis*.) — HACKBERRY, SUGARBERRY, NETTLE-TREE.

A genus of 50–60 species widely distributed in temperate and tropical regions of the world, with five species in our range. Because of the common occurrence of intergrading forms, as well as ecological variations, the species are at best poorly defined and are much in need of careful biosystematic study. The species enumerated here should be considered as tentative. Many of the minor variants have been described at various subspecific levels.

Combining mainly vegetative and floral characters with geographical distribution Planchon divided *Celtis* into four subgenera, two of which, CELTIS and MOMISIA, are represented in our area. Subgenus SPONIOCELTIS, composed of three species with linear, entire stigmas, the flowers borne in cymes with the staminate and/or polygamous flowers borne near the apex of the branchlets, is disjunctly distributed in tropical America and Malesia. *Celtis Swartzii* Planch., of the Greater Antilles, is closely related to the Malesian *C. cinnamomea* Lindl., but *C. trinervia* Lam., attributed to this subgenus by Planchon appears to be placed better in

subgen. CELTIS. Subgenus SOLENOSTIGMA Planch., characterized by two-lobed or emarginate stigmas and the flowers borne in cymes, is restricted to southern Asia and Australia. The monotypic genus *Mirandaceltis* A. J. Sharp was established for *C. monoica* Hemsl., of Mexico, which differs in leaf venation and drupe size and which is perhaps somewhat intermediate between *Celtis* and the Asiatic genus *Zelkova*.

Subgenus CELTIS (subgen. *Euceltis* Planch.), widespread, mostly throughout the mild-temperate regions of the world, is characterized by linear, entire stigmas and staminate flowers fasciculate in the axils of new leaves. Three species occur in eastern North America. *Celtis laevigata* Willd. (*C. mississippiensis* Bosc), $2n = 20$, with drupes 5–8 mm. long and narrow entire to somewhat serrate leaves, ranges from southeastern Virginia, south through Florida, and west to southern and western Texas, northeastern Mexico and southeastern Oklahoma, southern Kansas, Missouri, southern Illinois, southern Indiana, and central Kentucky. Varietas *Smallii* (Beadle) Sargent (*C. Smallii* Beadle), of questionable status, differs only in its constantly serrate leaves. Shorter, thicker leaves and more pubescence dubiously separate var. *texana* (Scheele) Sarg. (*C. texana* Scheele) from var. *laevigata*. A shrub or small tree, generally of exposed habitats, with drupes 5–8 mm. long and relatively small, often entire leaves, *C. tenuifolia* Nutt. is found from southeastern Pennsylvania to Indiana, northern Illinois, Missouri and eastern Kansas and south to eastern Oklahoma, Louisiana and northern Florida. Fernald & Schubert distinguished var. *georgiana* (Small) Fern. & Schub. (*C. georgiana* Small) on the basis of its pubescence and leaves which are coriaceous and scabrous above. A third species in our range, *C. occidentalis*, $2n = 20, 28$, has a more northern distribution, ranging from Massachusetts and New Hampshire to New York, southern Quebec, southern Ontario, central Michigan, southern Manitoba, Minnesota and central North Dakota, south to western Nebraska, northeastern Colorado, southeastern Wyoming, western Kansas and western Oklahoma, east to Arkansas, Alabama, and Georgia. Varietas *pumila* (Pursh) Gray (*C. pumila* Pursh) is based on plants with submembranaceous to membranaceous leaves which are conspicuously inequilateral at the base. Boivin (1967) described var. *Soperi* from southeastern Ontario and from northern Illinois on the basis of the leaves being regularly dentate. Other species within the continental United States which are assignable to this subgenus are *C. Lindheimeri* Engl., of central and southern Texas, and *C. reticulata* Torrey (*C. Douglasii* Planch.), of the western states (Wyoming and Idaho, west to western Washington, south to Oregon, eastern and southern California, east to Arizona, northern Mexico, New Mexico and western Texas, western Oklahoma, and Colorado).

Subgenus MOMISIA (F. G. Dietr.) Planch. with about 15 species in the Neotropics, is centered in Brazil and attains its northernmost limits in southern Florida and the southwestern United States. The flowers have linear, bifid or twice bifid stigmas, and they are borne in racemes. Typically shrubs, the species usually have solitary or paired axillary spines

in the stipular position. *Celtis iguanaea* (Jacq.) Sarg. (*Momisia iguanaea* (L.) Rose & Standl., *M. aculeata* (Swartz) Klotzsch) is reported from the southwestern coast of Florida and the Coastal Plain of Texas. The smaller- and scabrous-leaved *C. pallida* Torr. (*Momisia pallida* (Torr.) Planch.), common in central, western and southern Texas, New Mexico, Arizona, and in Mexico from Chihuahua to Baja California south to Oaxaca, is also known from the western coast of peninsular Florida.

Chromosome numbers reported for *Celtis* (six species) are $2n = 20$, 22, 26, 28, and 40. Sax noticed in *C. occidentalis* very irregular meiotic divisions with little pairing and with the univalent chromosomes irregularly distributed. Although 80 per cent of the pollen was sterile, a large number of fruits were produced. As Sax indicated, if the species contains two different basic sets of chromosomes with only a few homologous chromosomes or parts of chromosomes it could breed true only by some form of apomixis, a problem in *Celtis* that has not been investigated, but one which may be crucial in the taxonomy of the genus.

Flowering of *Celtis* species begins with or shortly after the appearance of the leaves in early April to late May. The drupes, ripening in September and October, are dark red to purple and are often sought after by animals. The fruits are eaten principally by birds, which in turn aid in the dissemination of the hard stones.

Numerous fossilized stones of the drupes of *Celtis* have been discovered in Europe, in Asia (including Japan), and in the western, midwestern, and southern United States. The first records are apparently from the early Eocene in Wyoming and the late Eocene in Georgia (United States) with only one European species. Continuing through the Oligocene, *Celtis* species are best known from the Miocene (at least nine species). Fossilized material of *Celtis* from the Pliocene is sparse, and even less is known of the genus in the Pleistocene.

Perhaps the most obvious disease of hackberries is the characteristic "witches-broom" produced by numerous proliferations at the branch tips. Although the cause is not clearly understood, a mite, *Eriophyes*, and the powdery mildew *Sphaerotheca phytophylla* are almost consistently associated with outbreaks of the deformations. No effective control is known. Although at least 17 types of insect galls occur on *Celtis occidentalis*, four caused by species of the genus *Pachypsylla* (Hemiptera) appear to be most prevalent. Damage to the trees is probably slight, even though the adults overwinter in the cracks of the bark. More serious threats, when abundant, are the spiny elm caterpillar, which is the larva of the mourning cloak butterfly, *Nymphalis antiopa*, and the larva of the hackberry butterfly, *Chlorippe celtis*, both of which feed upon the leaves. The hackberry engraver beetle, *Scolytus muticus*, often is found on the dead or dying branches.

The wood of both species is clear, light yellow with a thick, lighter-colored sapwood, but that of *C. occidentalis* is coarse grained, while that of *C. laevigata* is described as close grained. The secondary xylem is

also characterized by thin medullary rays and numerous small groups of small ducts arranged in intermediate concentric rings. In a comparison of the wood of temperate and tropical species of New and Old World *Celtis*, Cox and Grumbles independently showed that the species of temperate areas were ring-porous, while the tropical species were diffuse porous, an obvious reflection of the effects of seasonality on the trees. Only *C. occidentalis* and *C. laevigata*, of the species in our range, are large enough for the rather soft, weak wood to be utilized to any extent. The wood is used largely for posts, inexpensive furniture, boxes, crates, barrels, and other miscellaneous items. Described as a good tree for shade, species of *Celtis* are planted as yard and street trees. At least seven taxa, mainly from southeastern Asia and China, have been introduced into the United States.

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4. **Trema** Loureiro, Fl. Cochinch. 562. 1790.

Evergreen trees or shrubs of tropical forest margins and disturbed areas, the bark usually lightly fissured; branchlets terete, unarmed, variously pubescent, usually with conspicuous lenticels; buds axillary, narrowly ovate, covered with thin imbricate scales. Leaves distichous in ours, petiolate, variously serrate [to subentire], pinnately veined, usually conspicuously 3-veined at the base, the veins prominent beneath; stipules free, lateral, subpersistent to persistent [caducous?]. Plants monoecious [subdioecious], the flowers imperfect or polygamous (but then functionally imperfect), articulated with the pedicel, in axillary, subsessile cymes. Staminate flowers with the perianth 4- or 5-lobed, the lobes united near the base and induplicate-valvate or slightly imbricate; stamens 4 or 5, the filaments flattened, included to equalling the perianth lobes, the anthers introrse, ovate, dorsifixed below the middle; pollen 2-porate, suboblate, a rudimentary ovary usually present with numerous hairs at its base. Carpellate flowers with 4 or 5 flattened perianth lobes, the lobes united near the base, ± imbricate; style central, divided to the base, the two branches linear, minutely plumose-stigmatic on the inner faces; ovary sessile with numerous pilose hairs inserted at the base, 1-loculate, ovule

FIG. 2. **Trema.** a–i, *T. micrantha*: a, branch with staminate flowers, × ½; b, same, leaves removed, × 2; c, staminate flower with rudimentary gynoecium, × 5; d, node with carpellate flowers, leaf removed, × 2; e, carpellate flower, × 10; f, same, vertical section, semidiagrammatic, × 10; g, mature fruit, × 5; h, seed, × 10; i, same, in partial section to show embryo, × 10. j, *T. Lamarckiana*, leaf, × ½.

amphitropous; stamens wanting. Drupe small, ovoid or subglobose, inclosed basally by the persistent perianth, often beaked by the persistent style, smooth [pitted]; exocarp ± fleshy, endocarp hard; seed with fleshy endosperm. Embryo curved or nearly involute; cotyledons narrow, radicle folded inward and ascending. (*Sponia* Comm.) TYPE SPECIES: *T. cannabina* Lour.; for discussion of the identity of the type and appropriate synonyms see E. D. Merrill, A Commentary on Loureiro's "Flora Cochinchinensis" 132, 133. 1935. (Name Greek, *trema*, hole, in reference to the sometimes pitted drupe.)

A primarily pantropical genus of some 45 to 55 species with two, *Trema Lamarckiana* (Roem. & Schult.) Blume and *T. micrantha* (L.) Blume (*T.*

floridana Britton) occurring in our area. *Trema Lamarckiana* is found in southern Florida (Dade and Monroe counties), including the Florida Keys, and from Bermuda and the Bahamas to the Greater Antilles and into the Lesser Antilles from Saba to St. Vincent. Readily distinguished from *T. Lamarckiana* by its larger leaves which are not scabrous beneath, *T. micrantha* is widespread in the West Indies and coastal Mexico southward to Central and South America and occurs in our area from the Florida Keys northward to central peninsular Florida. The species of *Trema* are highly variable and often confusing, and the taxonomy of the genus is poorly understood.

Characterized by their spreading crowns and horizontal to slightly drooping branches, species of *Trema* are generally secondary forest trees and usually indicators of secondary succession. In a study of succession in old clearings on Barro Colorado Island (Panama), Kenoyer (1929) found that *T. micrantha*, along with *Cecropia*, *Apeiba*, *Ochroma*, and *Cordia* were the first trees to establish themselves. Other species of *Trema* have been reported as secondary forest indicators or major components in various stages of secondary succession in western Africa and Malaya. The rapidly growing trees are also found along forest margins and in disturbed areas, both natural (e.g., gravel bars) and man-made (roadsides).

Cytologically the genus is poorly known. The chromosome number of *Trema orientalis* Blume has been reported as $2n = 20, 36, 40$ and that of *T. cannabina* as $2n = 40$. Anatomically *Trema* is closely related to *Celtis*. Of the ulmaceous genera tested by Stake (1931) only *Trema* and *Celtis* had cystoliths in the upper epidermis, mainly in association with the hairs. Mucilage cells are common in the mesophyll of all species of *Celtis* and of many of *Trema*, but are lacking in the two *Trema* species in our range. Little is known of the embryology and floral biology of *Trema*.

Flowering and fruiting appear to occur throughout most of the year with the flowers often noticeable in early spring (late March and early April). The minute greenish flowers are soon followed by tiny orange to bright yellow (?) drupes. The wood has been described by Little & Wadsworth (1964) as light brown, soft, weak, lightweight and of limited use. In Puerto Rico the wood is occasionally used for fence posts and fuel and the strong fiber in the bark for cordage. The inner bark is light brown or pinkish and is tasteless to slightly bitter.

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ARNOLD ARBORETUM
OF
HARVARD UNIVERSITY

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 10. NOTES ON TWO SPECIES OF MARCGRAVIA

RICHARD A. HOWARD

THE TYPE GENUS *Marcgravia* of the Marcgraviaceae is familiar to collectors in the American tropics for its conspicuous heteroblasty and for the development of pedicellate saccate nectaries at the apex of the dense racemose inflorescence, the flowers of which usually form a distinctive umbellike cluster. The plagiotropic juvenile shoots of all species of *Marcgravia* examined in the West Indies have distichous leaves arranged on flattened stems which spread over the ground, over and on boulders, and up the trunks of trees (FIGURE 1). Although the juvenile leaves vary in form and size, they have characteristics which permit them to be identified with particular species. In most species the juvenile leaves are subsessile and often overlap the stem (FIGURE 1a). Numerous adventitious roots develop in rows from the stem beneath the leaves and afix the young shoot to the substratum (FIGURE 1b). Sir Hans Sloane in 1707 illustrated the climbing shoots and indicated that they were sterile and that he was unable to associate them with known plants. He listed them with ferns and aroids. With increasing age and with unknown factors of maturity, freely arching orthotropic branches lacking adventitious roots develop from the axils of the juvenile leaves (FIGURE 1c). These axillary stems bear leaves of entirely different size and shape. The apex of the climbing juvenile shoot may also change suddenly, or with transitional phases, to the production of leaves of the mature form, usually when freed by weight or other forces from the substratum. The terminal free shoot or the axillary branch may, upon contact with the trunk of a tree or other substrata, revert to the juvenile leaf form. Examples have been found, and even reproduced in a greenhouse, of the repeated transfer of a single stem from juvenile to mature form and back again (FIGURE 1d).

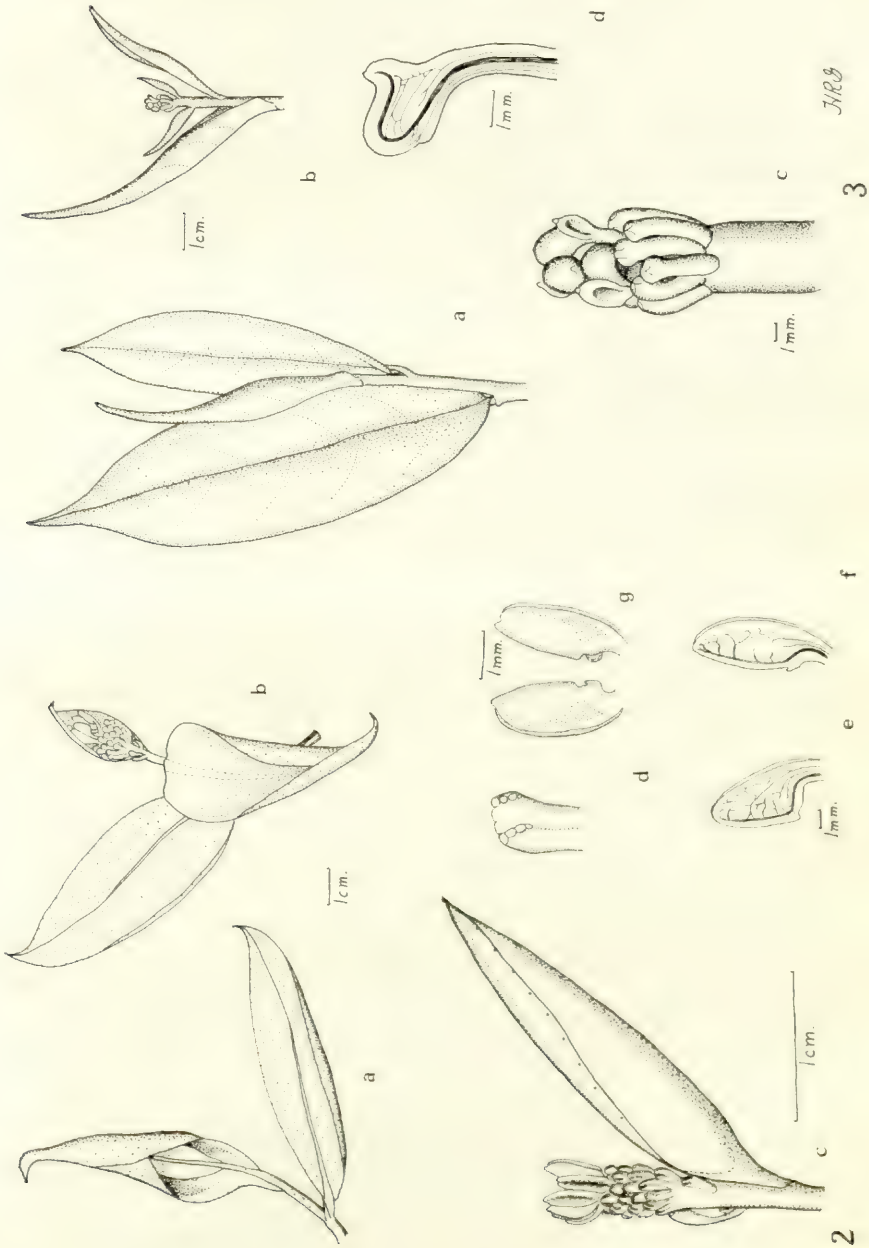
Stems of *Marcgravia* may reach the canopy of an elfin forest and extend over the crowns of other plants or ascend the trunks of forest trees, forming masses in the branches of the crown, and produce long axillary shoots, pendent or reaching nearly to the ground.

The inflorescence of species of *Marcgravia* in the West Indies is developed terminally on the axillary branches. After flowering and producing fruit, the flowering branch may die back a few internodes before an axillary bud on the same branch develops into a new shoot, continuing the elongation of the primary axis. The apical meristem of *Marcgravia* is surrounded and protected by overlapping leaves which form a slender pointed bud, enlarged at the base (FIGURE 3a). In primordial stages the leaf is terminated by a relatively large multicellular gland often conspicuous in the terminal bud (FIGURES 2c, 4c, 5c). Similar glands may be found along the margin of the lamina (FIGURE 2c). These glands are con-

FIGURE 1. A plant of *Marcgravia sintenisii* grown in the greenhouse of the Arnold Arboretum in Jamaica Plain, Massachusetts. a. Plagiotropic stem with juvenile leaf-form appressed to brick wall of greenhouse. b. Adventitious roots of plagiotropic stem visible where leaf has been removed. c. Axillary orthotropic stem showing abrupt transition from juvenile leaf form to adult leaf form. d. An orthotropic stem which changed from the basal juvenile leaf form to the adult leaf form and reverted to the juvenile leaf form on plagiotropic stems when appressed to the wall.

FIGURE 2, left. *Marcgravia sintenisii*. a. Orthotropic stem apex with flower bud. b. Leaves removed to show young inflorescence. c. The inflorescence is a raceme. The nectary-bearing pedicels are contiguous with the flowering pedicels at this stage of development. Marginal hypophyllous glands are shown on the leaf. d. Young flower bud showing large marginal glands of the incipient perianth parts. e, f. Cleared nectaries. g. Two young nectaries showing the aborted flower bud.

FIGURE 3, right. *Marcgravia rectiflora*. a. Orthotropic stem apex with flower bud enclosed in leaves. b. The young inflorescence with nectary-bearing pedicels clearly differentiated at the apex of the raceme. c. The young inflorescence. d. A cleared young nectary showing the early stages of invagination and distortion.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spicuous in the juvenile leaf form and appear to remain functional for a long period of time. In the adult leaf form the terminal and marginal glands become brown and hard at an early stage of development. Large hypophyllous glands are found in characteristic patterns on the leaf blade, associated with the midvein or localized in particular spots on the lamina (FIGURES 4, 5).

The terminal bud containing a young inflorescence is only slightly more swollen initially than the vegetative bud. There is only a slight reduction in leaf size immediately below the inflorescence. In the raceme the flowering pedicels are borne in a dense spiral, but the axis is terminated with the development of pedicels dominated by the lateral saccate nectary which has its orifice at the base (FIGURES 2c, 3c). The development of the terminal nectary-bearing pedicels is precocious in comparison with the flowering pedicels. The flowering pedicels are ascending in relation to the axis in the young buds and the flowers are borne apically on the pedicel. With continued development the flowering pedicels tend to diverge from the inflorescence axis, in some species to a 90-degree angle, or even to become slightly reflexed. The apical flower primordium retains the same axis as the pedicel in the subgenus ORTHOTHALAMIUM (Wittmach, 1878). In other species forming the subgenus PLAGIOTHALAMIUM the flower bud is offset from the apex and may be at a 90-degree angle to the axis of the pedicel.

In many species, as in *Marcgravia rectiflora*, the flowering axis remains erect and the flowers ascend (FIGURE 6). The terminal nectary-bearing pedicels, therefore, recurve to varying degrees so that the basal opening of the nectary is oriented upward. In other species, as represented by *Marcgravia sintenisii*, the inflorescence axis is pendent so that the flowering pedicels form an umbel with the flowers pointed downward (FIGURE 7). The axis of the nectary-bearing pedicels, therefore, is not distorted and the basal opening of the nectary is directed upward. This is the characteristic "wheel" of hanging flowers so frequently illustrated as typical of *Marcgravia*, which has given rise to suggestions and speculations that the plants are pollinated by humming birds hovering beneath the open flowers and becoming dusted with pollen while obtaining nectar from the saccate ovaries.

Within the many species of *Marcgravia* nectary-bearing pedicels show considerable variation. The nectary may be nearly as long as the pedicel and is then often described as sessile, or it may range from three-fourths to only one-fourth the length of the pedicel. The majority of species have elongate cylindrical nectaries with an asymmetrical orifice and lip, a narrowed neck, and a swollen base. A few species have flattened and broadened nectaries, described as galeate but to be considered so only when the inflorescence axis is ascending. The terminal pedicels producing nectaries may also bear a minute or abortive flower, suggesting that they are but modifications of the lower, nectary-less, flowering pedicels.

The nectary-bearing pedicels do not persist long after the flowers have shed their calyptrate corollas. No fruiting specimens were found in the

wild or in herbarium collections with the nectary-pedicels remaining attached. Since the shape of the nectary is a character of taxonomic importance, the need for collections of flowering material is apparent.

The morphology of the nectary and its role in pollination are controversial and still undetermined in the available literature for many of the species. Additional field observations are needed. Patrick Browne, in *The Civil and Natural History of Jamaica*, published in 1756, observed on *Marcgravia* that "this curious plant is frequent in the woods of *Jamaica*; and appears in such various forms, that it has been often mistaken for different plants, in the different stages of growth." Of the inflorescence he reported, "The flowers are sustained by long foot-stalks, and disposed in the form of an *umbella*, about the extremities of the branches; but the summit, or crown of the supporter, is constantly adorned with four, five, or more hollow, divergent, glandular bodies, that occupy the center of the *umbella*: these are of an arched oblong form, obtuse and roundish; they are hollow within, and affixed by very short foot-stalks, that rise immediately from one side of the aperture, or opening of the gland; which is

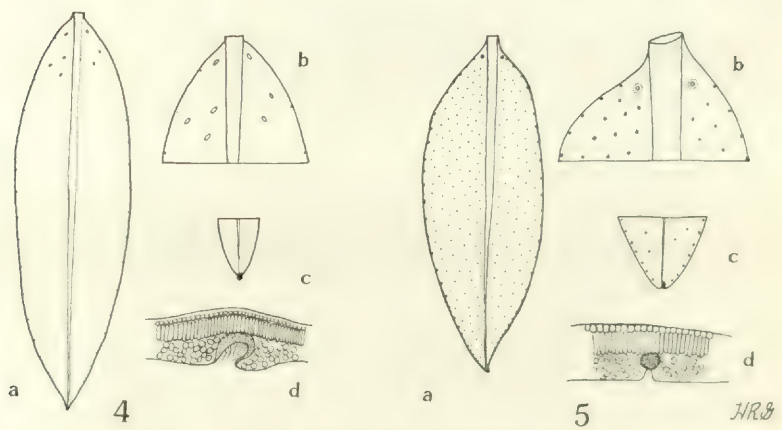


FIGURE 4, left. a, b. Leaf of *Marcgravia sintenisii* showing the several hypophyllous glands near the base of the lamina. c. The terminal gland of young leaf. d. Diagrammatic section of the leaf blade through a gland.

FIGURE 5, right. a, b. Leaf of *Marcgravia rectiflora* showing the two large glands near the base of the lamina. c. Apex of young leaf. d. Diagrammatic section of the leaf blade through a gland.

so disposed, as to receive the water that dribbles down along the branch in rainy weather. What the real use of these may be, is not easily determined: it is, however, remarkable, that the leaves of the branches are plain, of an oblong oval form, with a smooth membranous edge; while those of the younger plants are always observed to have many little glands, set gradually round the margin."

Thomas Belt, author of *The Naturalist in Nicaragua*, published in 1874,

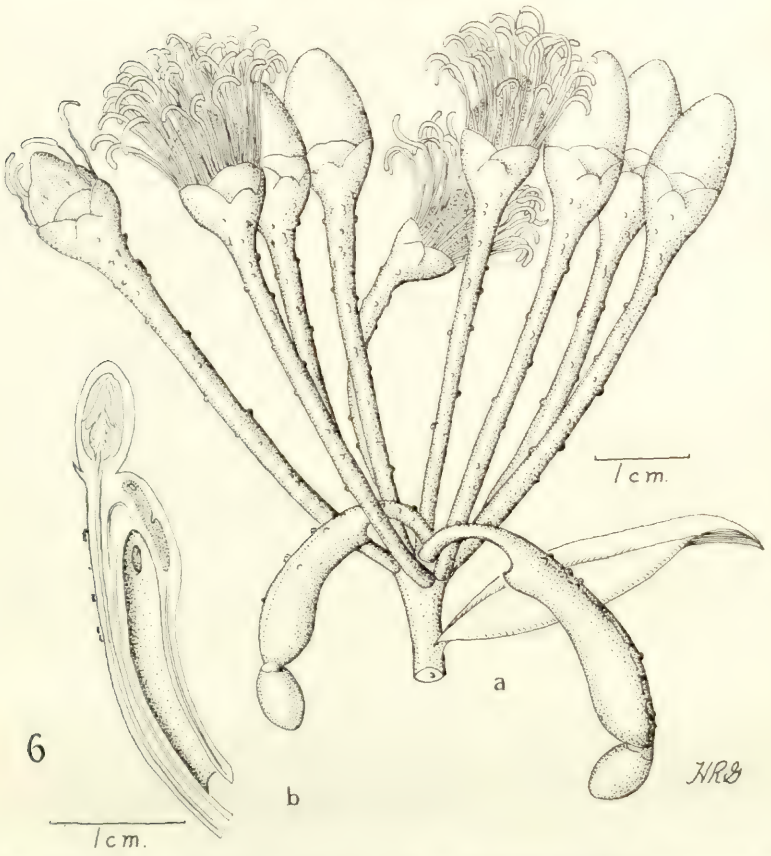


FIGURE 6. a. The erect inflorescence of *Marcgravia rectiflora*. Flowers show the two bracts subtending a four-parted calyx, the calyptrate corolla, and the numerous stamens which have shed pollen before the fall of the corolla. The elongate nectaries are on terminal but recurved pedicels. In this clone the flower bud of the nectary-bearing pedicel has not aborted, but does not mature. b. Diagrammatic representation of the nectary-bearing pedicel. The area of glandular tissue and one of the two pores is shown. The unaltered bract comparable to the modified nectary bract is also shown.

is considered to be the originator of the humming-bird pollination legend. He reported of *Marcgravia nepenthoides*, "The flowers of this lofty climber are disposed in a circle, hanging downwards, like an inverted candelabrum. From the centre of the circle of flowers is suspended a number of pitcher-like vessels, which, when the flowers expand, in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds, including the species I have mentioned and many kinds of hummingbirds. The flowers are so disposed, with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another.

A second species of *Marcgravia* that I have found in the woods around Santo Domingo has the pitchers placed close to the pedicels of the flowers, so that the birds must approach them from above; and in this species the flowers are turned upwards, and the pollen is brushed off by the breasts of the birds." This story has been rewritten, applied to other species without verification in many subsequent volumes, although most recently qualified by Meeuse (1961) who states, "In all likelihood birds are the normal pollinators in *Marcgravia*, although bat pollination is suspected in a few cases." A paper by I. W. Bailey (1922) entitled "The pollination of *Marcgravia*: a classical case of ornithophily?", which questioned the general acceptance of humming-bird pollination, has been generally overlooked. Bailey examined several species of *Marcgravia* in British Guiana and concluded the flowers are self-fertile or autogamous, instead of being protandrous and cross-pollinated by birds. He found that inflorescences would set fruit when enclosed in protective cloth which excluded any birds, and he reported that other inflorescences produced fruit under water.

During a recent period of field study in eastern Puerto Rico two species of *Marcgravia* representing the two subgenera and matching the types described by Belt were available in quantity for frequent observation. One species endemic to Puerto Rico, *Marcgravia sintenisii* (FIGURE 7), occurs frequently at higher elevations in the Luquillo Mountains and was in the Pico del Oeste study area (Howard 1968). A second species, *Marcgravia rectiflora* (FIGURE 6), has a wider range of distribution including Cuba and Hispaniola, and is reported from South America; it occurs at a lower elevation in Puerto Rico, primarily along the Rio Cubuy in the Luquillo Mountains.

The species may be contrasted in other ways. *Marcgravia sintenisii* occurs in and on the canopy of the elfin forest. It has a pendent inflorescence developed at the apices of short axillary branches. The flowers, therefore, hang and the stamens are exposed from below. The nectaries are flattened and galeate in normal position but appear flat-topped at the orifice and obtuse at the base, as observed in the flowering condition (FIGURE 7d). The nectaries are pale yellow-orange in color until the corolla cap is ready to break free, when they turn a brilliant red. The flowering pedicels number 30 to 60 and the nectary-bearing pedicels about nine to eleven. The corolla caps fall in the early morning hours and the stamens diverge from the pistil by adaxial growth or elongation. The stigma appeared to be receptive, i.e., glistening and dusted with pollen at the time of abscission of the corolla cap, and within an hour or two after opening the anthers had shed all pollen and begun to wither. The flowers did not mature in sequence according to their position on the axis, but one radial group appeared to shed the corollas, followed by another segment often separated from the first by flowers slower in development. The whitish filaments persisted but were easily dislodged at this stage. Although it appears that the flowers are pollinated in bud, the inflorescence as a whole had still unopened flowers at the same time other flowers had already lost their stamens. In the course of observations made over a period of three

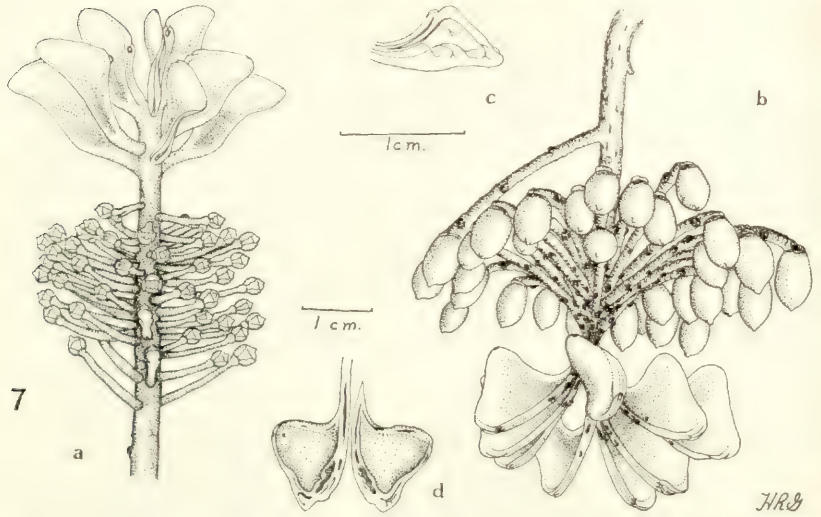
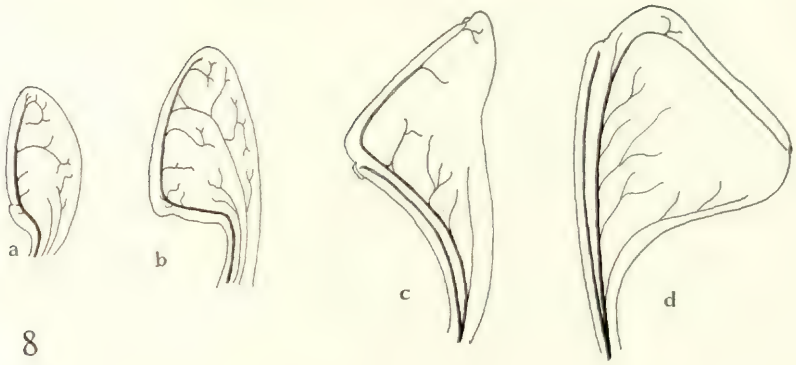


FIGURE 7. *Marcgravia sintenisii*. a. A young erect inflorescence showing the elongation of the axis between the flower-bearing pedicels and the nectary-bearing pedicels. The young flower buds are oriented with the axis of the pedicel. Aborted flower buds are shown on the nectaries. b. The mature inflorescence is pendent. The angle of the flowering pedicels has been altered in development and the flower is now at right angles to the axis of the pedicel. Further shift in orientation of the nectary is evident. c. Diagram of cleared young nectary showing the aborted flower bud. d. The inverted galeate nectary split to show the glandular tissue.

years we noticed that the inflorescences were visited by the green-throated hummingbird (*Sericotes holosericeus*), by Todies (*Todus mexicanus*), and by bees seeking nectar from the orifice of the nectary. The most frequent visitor, however, was the bananaquit (*Coereba flaveola*) which grasped and hung from the brilliantly colored nectaries and pecked at the base (morphological apex) creating sizeable holes in and through the tissue of the nectary. Subsequently the bees also visited these injured areas instead of approaching the nectaries at the natural orifice.

Marcgravia rectiflora is a stronger climbing plant of greater volume, which does not reach the canopy of the forests of lower elevations but seems to dominate many of the host trees by growing luxuriantly on the lower branches. The lateral branches of this species are exceedingly long and pendent, some reaching 15 feet and showing as many as 25 inflorescence scars. The inflorescence in *Marcgravia rectiflora* also develops terminally, but instead of hanging the tips of the branches turn upwards (FIGURE 6). The raceme, therefore, is morphologically erect and the flowering pedicels ascending. The nectaries developed on the terminal pedicels are strongly recurved and hang between the flower-bearing pedicels so that the opening of the nectary points skyward. The nectaries of *Marcgravia rectiflora* are elongate saccate structures larger at the base than at the orifice and nar-



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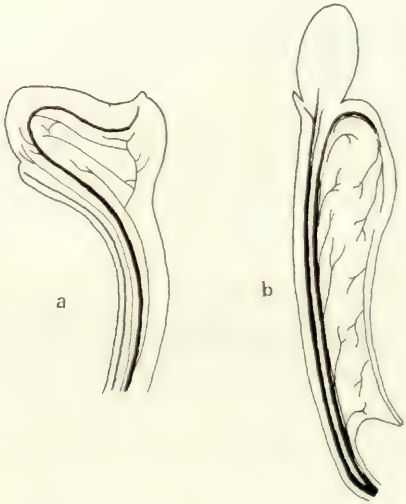

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FIGURE 8, above. Four diagrams to represent the transitions in form of the developing nectaries of *Marcgravia sintenisii*.

FIGURE 9, below. *Marcgravia rectiflora*. a. A young nectary-bearing pedicel showing the paired vascular strands, one to the aborted flower bud, the other showing the recurved path associated with invagination of the bract. b. A diagram of the vascular pattern found in the clone of *Marcgravia rectiflora* showing the early departure of the vascular supply to the nectary-bract, contrasted with the vascular supply to the normal bract and the flower bud.

rowed to a neck in the middle. The orifice is asymmetrical and the lip slightly recurved and pointed. The flowers number about nine to eleven and the nectary-bearing pedicels about four. The flowers are three to four times the size of those of *Marcgravia sintenisii* and shed the calyptrate corolla in a similar haphazard pattern, unassociated with the position of the flower on the inflorescence axis. Again, the stigmatic area was glistening and possibly receptive when the corolla-cap fell. The stamens also

spread widely, but the anthers shriveled within a few hours and became dark brown. The filaments were easily detached.

The position of the nectaries of *Marcgravia rectiflora* in relation to the flowers is such that pollination can not be effected by a hovering hummingbird in the theoretical manner but could occur in the way that Belt described birds acquiring pollen on their breasts from erect flowers. In fact no hummingbirds or todies were seen to visit the inflorescences of *M. rectiflora* in the course of many hours of observation. The bananaquit, however, was a frequent visitor, here landing in the middle of the inflorescence, forcing its way to the recurved nectary-bearing pedicels, and tipping its beak into the nectary. The bananaquits also managed to tear the nectaries from the orifice to the base, laying open the glandular tissue, or literally removing the globular end of the nectary. In the process of this activity the bananaquits brushed against many of the open flowers, and stamens were dispersed in all directions. It is possible that cross-pollination between newly opened flowers could be effected in this manner. Subsequently, bees which visited the inflorescence took advantage of the injured nectaries and approached the damaged tissue area directly from well below the flowers. In contrast to those of *Marcgravia sintenisii*, the nectaries of *M. rectiflora* do not develop a brilliant color but remain green and brown.

Bees, wasps, and hornets which visited the young inflorescences of *Marcgravia rectiflora* did not approach the cluster of flowers from above but landed below the flowering pedicels and worked their way up the axis to the nectary glands. In many cases the bees, wasps, and hornets did not bother with the nectary orifice but confined their feeding to the "corky" excrescences developed on the pedicels or on the outer surface of the saccate nectary.

During the course of frequent observations it was noted that the hanging axillary branch and the inflorescence of *Marcgravia rectiflora* were the preferred territory of an anolid lizard (*Anolis evermanni*), which spent many hours on successive days in the middle of the inflorescence, but scrambled back up the stem at times while foraging. Like the bananaquit, the lizard was seen to crawl over open flowers and to break off stamens. It is interesting to speculate that a few flowers of *Marcgravia rectiflora* were pollinated by an anolid lizard. The anolid found the inflorescence a good hunting area and was seen to catch small insects apparently approaching the flowers. On one occasion the anolid caught a butterfly, but the other insects remain unidentified.

Mr. Henry Draper, with the aid of a telephoto lens, was able to record an anolid lizard with its snout in the orifice of one of the nectaries. Again the lizard probably was not supping on the nectar but catching small red-brown ants and mites which have been found within the nectaries in subsequent dissection. The lizard was missing from his favorite territory one afternoon when I planned to watch his behavior again. Nearly an hour of observation time passed before I realized that his usual haunt was then occupied by a snake (*Alsophis portoricensis* or *Dromicos exiguus*). This

snake was stretched along the full length of the branch and its head was in the center of the inflorescence. Neither the snake nor the lizard was seen on this branch in succeeding days.

I. W. Bailey (1922) observed the flowering characteristics of several species of *Marcgravia* in British Guiana and found that bagged inflorescences set fruit, as did some stems that flowered under water. The natural fertility of the two species in Puerto Rico was also high. Several inflorescences that were covered tightly with bags of cheese cloth during the summers of 1966 and 1967 produced developing fruit on as high a percentage of the flowers as did unbagged inflorescences. Swamy (1948) supported Bailey's observation that the anthers of *Marcgravia* split and release pollen grains before flower anthesis. He also noted that a large percentage of the pollen had germinated at anthesis and that pollen tubes of varying length were found. Some pollen tubes were observed on pollen collected from open flowers of both species occurring in Puerto Rico. It seems unlikely that pollen grains which had developed pollen tubes could be transported any distance in the process of cross-pollination. Swamy reiterated Bailey's conclusion that the two species they studied were autogamous or self-pollinated. This seems to be true of the two species studied in Puerto Rico, *M. sintenisii* and *M. rectiflora*. In both species the anthers were open and pollen was shed within the bud before the calyptrate corolla had fallen. The stigmatic area, however, did not appear to be receptive until after the loss of the corolla, at which time it was glistening and covered with adhering pollen. Recently Meeuse (1961) suggested that *Marcgravia* may be pollinated by bats. No bats have been observed in the Pico del Oeste area by the individuals who participated in that study. Although the participants spent relatively few nights in this cloudy and cool area, it is hard to believe that bats would do so either. There are bats in the area where *Marcgravia rectiflora* was studied, and a reasonable attempt was made to observe the few open flowers of *M. rectiflora* in the predawn and late evening hours. No bats were seen to visit the inflorescences under observation.

Bailey pointed out in 1922, "There has been considerable speculation concerning the origin and morphological significance of these nectariferous appendages. Are they metamorphosed bracteoles, abnormal pedicels, modified bracts, or appendages *sui generis*? Most recent students of the Marcgraviaceae have accepted Planchon and Triana's (1863) conclusion that they are evaginated bracts. It must be admitted that there is considerable evidence in favor of this view." He then noted, as had Goebel (1905), that "the concave or inner surface of the nectariferous appendages is the morphological equivalent of the under surface of the leaves. The outlets or pores of the hypophyllous glands are located in this dorsal surface and, accordingly, discharge their sugary excretions into the concavities of the bracts." However, Bailey also concluded, "That the nectaries of Marcgravia are not abnormal pedicels, as maintained by Seemann (1870), but are compound structures resulting from the fusion of a nectariferous bract and a sterile pedicel, is indicated, not only by their

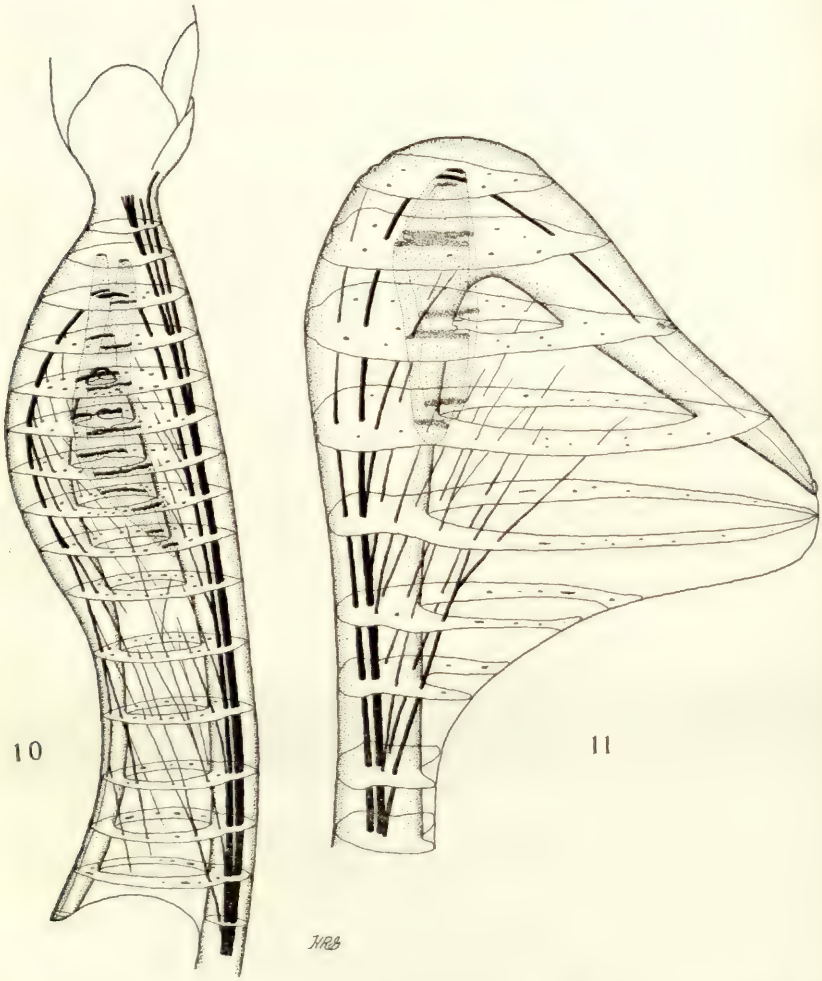


FIGURE 10, left. A diagrammatic reconstruction of the nectary-bearing pedicel of the clone of *Marcgravia rectiflora* which develops a flower bud. Preparation was made from cleared pedicels and from transverse sections. Two elongated hypophyllous glands are evident. The secondary vascular supply to the nectary area is derived from the full length of the bundle which ascends, curves over, and descends into the outer area of the flask-shaped nectary. The absence of a bract above the nectary contrasts with the presence of the opposing bract.

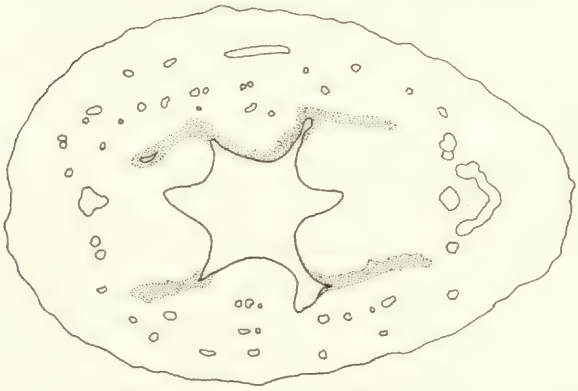
FIGURE 11, right. The galeate nectary of *Marcgravia sintenisii* diagrammatically reconstructed from cleared nectaries and from transverse sections. The small vascular strand to the aborted flower bud is shown. An ascending trace with secondary branches curves at the top of the nectary before descending to the morphological apex of the bract where a rudiment of the apical gland is shown. The flattened nectary has a wide orifice. Glandular tissue and its orifice are shown.

external morphology, but also by their internal anatomy." Bailey found "two distinct systems of fibro-vascular bundles in the nectaries, one belonging to the sterile pedicel and the other to the adnate bract." This statement is not completely accurate when applied to the two species used in the current study.

The floral structure of the two species of *Marcgravia* studied in Puerto Rico shows a calyx consisting of two pairs of overlapping, decussate sepals subtended and appressed by two smaller bracts (FIGURES 6, 7). In the flowering pedicel the vascular traces to these appendages depart from the central stele at about the same level and immediately below the vascular bundles which supply the corolla, androecium, and gynoecium. In the nectary-bearing pedicels, however, the flower is usually aborted and represented only by a small rudiment which has a very reduced vascular supply (FIGURES 8c, 9a). The bulk of the vascular tissue is directed to the nectary with the median bundle arching over at the apex of the nectary and descending to the lip and its terminal gland (FIGURES 8–11). Branch traces depart from both sides along the full length of this bundle, branching as they diverge into the body of the nectary. The vascular pattern can be observed readily in cleared nectary-bearing pedicels of *Marcgravia rectiflora*. (FIGURES 9b, 10). Numerous branched idioblasts and sclereids develop early in the nectaries of *Marcgravia sintenisii*, and in such profusion that only the main vascular bundles can be seen.

The secretive tissue is developed extensively in these nectaries. Bailey suggested that these were comparable to the hypophyllous glands found on the leaves, and the present observations support this conclusion. Two extensive areas of secretive tissue open through two pores in *Marcgravia rectiflora* (FIGURES 10, 12). Additional areas of secretory tissue, each with pores opening internally to the cavity, have been found in the nectaries of *M. sintenisii* (FIGURE 13).

The presence of rudimentary flowers at the apex of the pedicels which also bear the saccate nectaries has been noted frequently. Both Wittmack and Bailey illustrate pedicels in which the flower is of significant size and in some cases separated by a respectable distance from the nectary. One clone of *Marcgravia rectiflora* found and observed in Puerto Rico had well-developed flowers at the ends of nectary-bearing pedicels (FIGURES 6, 9, 10). The vasculature and glandular tissue of a nectary of this plant is illustrated (FIGURE 10). This clone was observed many times over a period of three years and there was no variation in the production of large flower buds. During development the flowers of the nectary-bearing pedicels and those without nectaries progressed at comparable rates until each was about two-thirds the mature size. At this point the flowers with subtended nectaries failed to increase further. The regular flowers enlarged, the corolla was shed, and fruit was set. The nectary-bearing pedicels fell off without the terminal flowers maturing or shedding the corolla. Examination of the flowers subtended by nectaries showed normal floral structure with well-developed stamens, the anthers of which contained mature pollen grains. When these structures were cleared and



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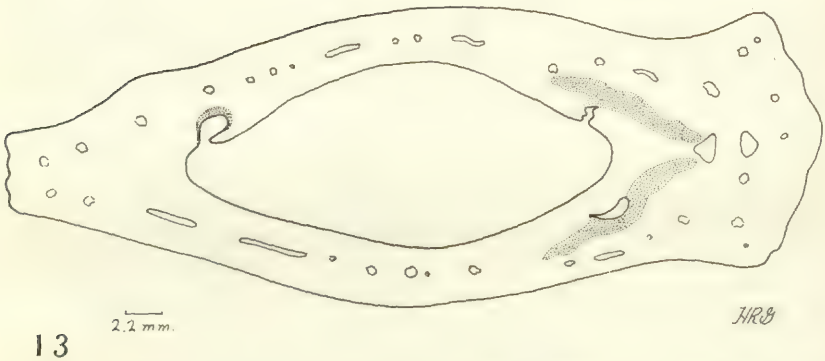

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FIGURE 12, above. A median transverse section of the nectary-bearing pedicel of *Marcgravia rectiflora* showing the opening into the cavity.

FIGURE 13, below. A median transverse section of the nectary-bearing pedicels of *Marcgravia sintenisii*. Three areas of glandular tissue are shown.

the vascular structure was examined, it was evident, as shown in the diagram (FIGURE 10), that a major vascular supply extended to the flower and that a branch of this system departed early, ran parallel to it, and ascended into the nectary area. This was conspicuous in contrast to nectary-bearing pedicels with abortive flowers where the vascular supply to the nectary surpassed in volume the vascular supply to the aborted flower. In each of the types of pedicels a single unit of vascular stele was present at the base of the pedicel, and the vascular supply to the nectary or the bract was but a branch of this central stele.

The normal flower of both species of *Marcgravia* has a four-parted calyx closely subtended by two bracts. The pedicels which bear nectaries, by contrast, possess but one normally developed bract opposite the

nectary area (FIGURE 10). The conclusion of Planchon that the nectary is a development of one of the bracts is verified. Although Planchon suggested this as an evaginated bract, the vocabulary of "fusion" or "adhering" remains in the literature. We have been able to examine a series of inflorescences of increasing age. FIGURES 2, 3, 8, and 9 show the adjustment in form that takes place in the maturation of the nectaries of both *M. rectiflora* and *M. sintenisii*. The distortion of form is gradual but consistent, leading to the respective saccate and galeate mature nectaries. The development pattern observed also supports the Planchon description of an invagination of one of the bracts which involves a distortion of the major part of the pedicel.

ACKNOWLEDGMENTS

I wish to acknowledge again the support of this study which was made possible primarily by a grant from the National Science Foundation (GB: 3975). A portion of the study was conducted on the property of Mr. Joseph B. Martinson in Puerto Rico; to him the collaborators in this study and I are grateful for generous hospitality. Patient observations over many hours were made by Judy Appenzeller; Mr. and Mrs. Henry Draper, and Madelon Gauer. Dr. and Mrs. Richard Wagner collected special materials following frequently repeated requests. Mrs. Helen Roca Garcia prepared the technical preparations and the drawings.

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ARNOLD ARBORETUM
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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 11. THE LEAFY HEPATICAE OF PICO DEL OESTE [1]

MARGARET FULFORD, BARBARA CRANDALL, AND RAY STOTLER

THE SUMMIT OF PICO DEL OESTE in the Luquillo Mountains of Puerto Rico, with an elevation of 1050 meters, is covered by an elfin forest or thicket from 2 to 5 meters high which in places, especially those covered by the low shrub, is almost inpenetrable, while in areas of taller trees the going is less difficult. In any case, the canopy is more or less closed throughout and even during sunny periods the light is diffuse. The rainfall is about 200 inches per year.

The area in which the collections were made has been under intensive

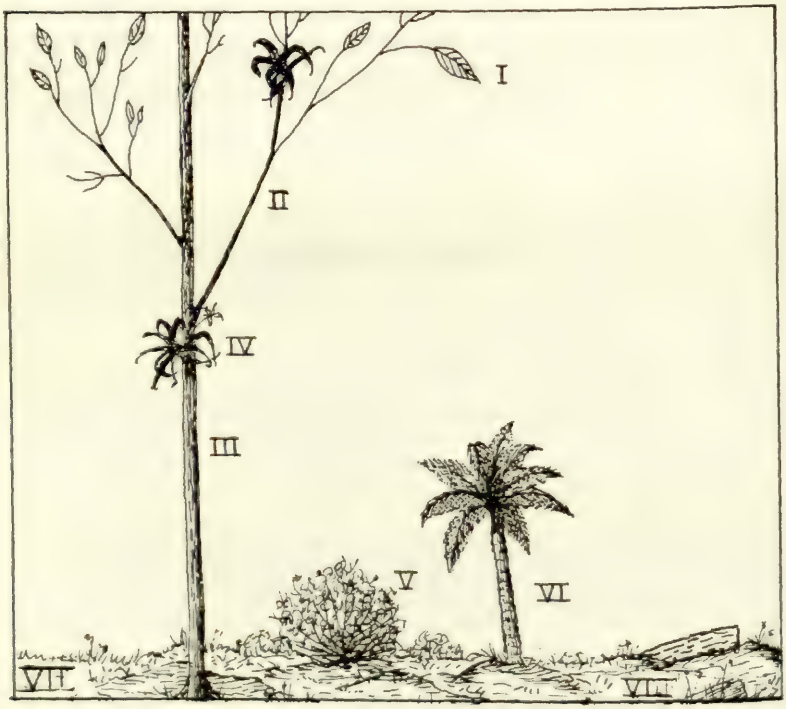


FIGURE 1. A diagram indicating the habitats and substrata available to leafy Hepaticae in the elfin forest: I, leaf; II, twigs and branches; III, trunk of tree; IV, bromeliad epiphyte; V, shrub; VI, tree fern; VII, the ground; VIII, log.

[1] Work relating to a project supported by National Science Foundation Grant, No. GB 7138, Margaret Fulford, principal investigator.

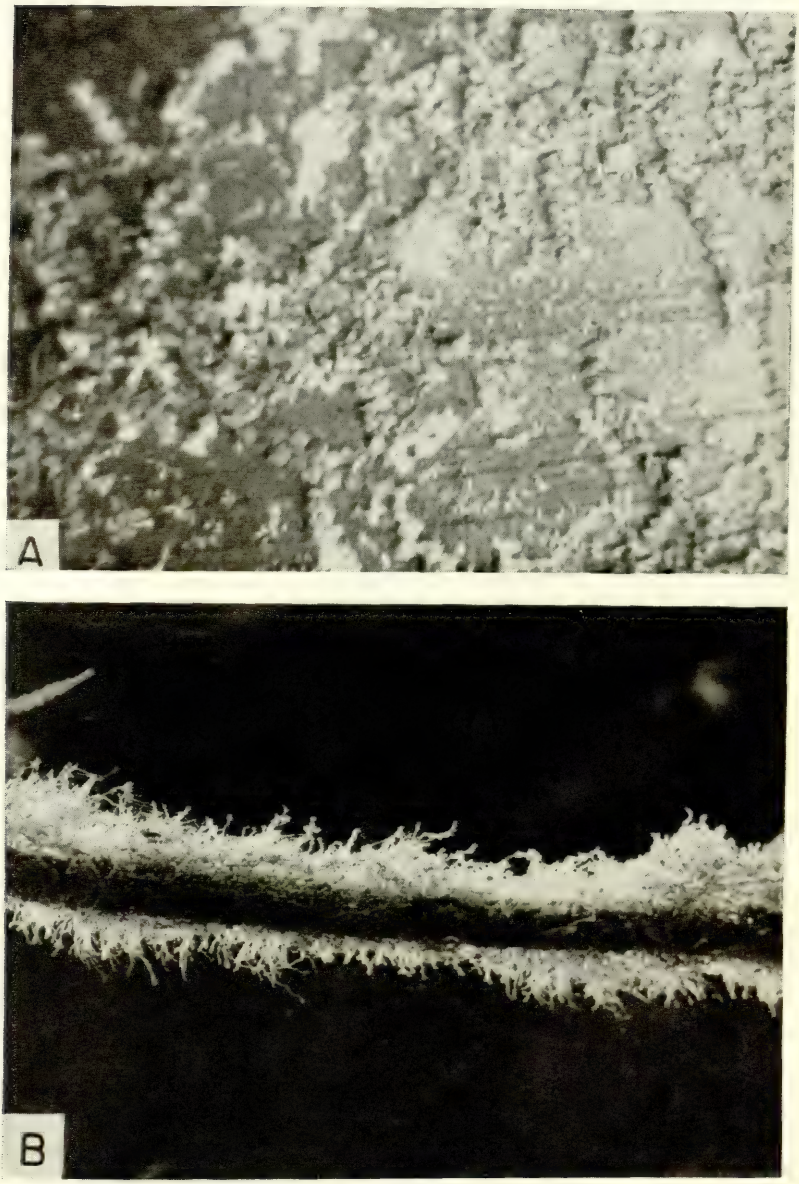


FIGURE 2A. Portion of a leaf covered with several species of leafy Hepaticae.
FIGURE 2B. Portion of a tree trunk covered with a loose mat of leafy Hepaticae.

investigation by Dr. R. A. Howard for a number of years and has already been described in detail (Howard, 1968). Most of our collections were made in the vicinity of his study trail.

As pointed out by many investigators (see Howard, 1968) such a type of woody vegetation has been variously described as elfin forest, elfin woodland, montane thicket, and mossy forest. At least in Puerto Rico, this "mossy forest" on Pico del Oeste, El Yunque, Mt. Britton, and El Toro, is mossy only in appearance, for leafy Hepaticae comprise 90 percent or more of the bryophyte flora of these areas. While the general aspect of the vegetation of these four peaks is similar (Howard, 1968), the actual composition of the leafy hepatic flora is different for each of them. This will be demonstrated in a later paper.

These leafy hepatics occupy all sorts of niches and substrata (FIGURE 1), and each may support several growth forms. The plants cover the ground, often in cushions up to a foot thick, cover the tree trunks and branches in large or small appressed mats, loose mats, deep tufts, large "balls" to 6 inches or more in diameter, or hang in festoons to two feet or more in length (FIGURES 2B, 3), or cover the leaves of the trees and shrubs, herbaceous plants, and ferns (FIGURE 2A).

In a general way, the variety of substrata and growth forms may be classified in the following manner:

I. LEAVES.
- a. Species with a tightly appressed growth habit, — in particular, young plants developing from discoid gemmae (gemmalings), in the genera *Colura*, *Cyclolejeunea*, *Diplasiolejeunea*, and *Radula*, or from tiny small-leaved branches in the genera *Drepanolejeunea*, *Prionolejeunea*, and others.
- b. Loose mats, usually on older leaves. Large colonies of the plants named under "a" show this form. Additional gemmae and tiny branches are caught in such mats.
- c. Tufts to 1 cm. high often become established within the older mats, especially the genus *Adelanthus*.

II. TWIGS AND BRANCHES.
- a. Appressed mats — of *Ceratolejeunea* spp., *Prionolejeunea* spp., *Frullania*, *Radula*, etc.
- b–c. Loose mats to deep tufts — of *Trachylejeunea*, *Bazzania longa*, *B. longistipula*, *Lepidozia patens*, *Plagiochila* spp., etc.
- d. "Balls" to 6 inches across — of *Bazzania stolonifera*, *B. breuteliana*, *Lepidozia patens*, *Plagiochila* spp.
- e. Pendent forms, to a foot or more long — of *Herberta*, *Cystolejeunea*, *Plagiochila* spp. and *Syzygiella*.

III. TREE TRUNKS.

These support a variety of growth forms, limited only by the time and space available. The forms and species are similar to those of twigs and branches.

IV. BROMELIAD EPIPHYTES.
- a. Appressed forms, especially small plants of *Colura*, probably developed from gemmae.

V–VI. SHRUBS AND FERNS.
- a. Appressed forms — on the leaves and petioles. The stems support the same

FIGURE 3. Tree trunks in the elfin forest with leafy Hepaticae in loose mats or pendent.

range of growth forms and species as are to be found on the tree trunks and branches.

VII. THE GROUND.

a. Appressed forms or low tufts — occupy spots of recently exposed soil, as *Alobiellopsis*.

b. Deep tufts and mounds — cover most of the area and form a deep, spongy, soggy, cushion over the forest floor.

VIII. LOGS.

a. Appressed forms — a few slender forms as *Nowellia*, *Telaranea* and *Cephalozia* soon become established but they are soon replaced by the rapidly growing larger species of the tree trunks and ground.

Most of the species are tinged with brown and some become bronze. A few are reddish to deep purple-black.

Many individual plants, especially those on leaves, are subjected many times a day, to a deluge of rain followed immediately by high wind, sun, and a rapid drying out, so that they survive frequent periods of xerophytism. This is particularly true of the unistratose, discoid gemmae and the gemmalings of the leaf-inhabiting species of *Colura*, *Cyclolejeunea*, and *Diplasiolejeunea* which are so abundant. Those plants in colonies are not so exposed.

Leafy Hepaticae may reproduce by spores, gemmae of various sorts, by specialized deciduous branches, by short, small-leaved branches, and by fragmentation of a stem or leaf. The first arrivals on a new leaf are, for the most part, the discoid gemmae of *Colura*, *Cyclolejeunea* and *Diplasiolejeunea*.

Both *Colura clavigera* (FIGURE 4) and *Cl. rhynchophora* (FIGURE 5a) have highly specialized leaves, for most of the leaf is an inflated water-sac with a special valve opening. Numerous insects are caught in these traps. The superficial unistratose, discoid gemmae develop from cells of the leaf (FIGURE 5a, G). The details of development of similar gemmae in other genera have been described by Evans (1911, 1912). There are usually three specialized cells on the margin which serve as "Haftorgane" or organs of attachment (FIGURE 5b, A). Such cells project at right angles to the surfaces of the gemma and the slime secreted from the tips serves to attach the gemma to the leaf. The new leafy plant develops through the activities of an apical cell which develops from a cell of the margin. The gemmae of *Diplasiolejeunea* (FIGURE 6a, b) are of the same general form.

In the genus *Cyclolejeunea*, perhaps the most widely occurring of the gemmiparous leaf-inhabiting taxa, gemmae develop from the marginal cells of the leaf (FIGURE 7a). The large discoid gemma of *C. convexistipa* (FIGURE 8), is unistratose and watch-glass shaped, and according to Evans (1904), apparently falls on the leaf with the concave side down and the margin appressed to the leaf surface, thus creating a water-holding space in the middle. Three or four long rhizoids and numerous short branched ones develop from the marginal cells. The latter are slime secreting and serve to anchor the gemma to the leaf (FIGURE 8, R). The

leafy stem develops from an apical cell on the margin. In *C. accedens* the gemma has only two long unbranched rhizoids (FIGURE 7b, R), bent over the lower surface, and an abundance of short, branched, slime-secreting marginal ones. The apical cell of the gemma gives rise to an oblong protonema or gemmothallus (FIGURE 7c, T), and the leafy plant develops from the margin of this latter thallus.

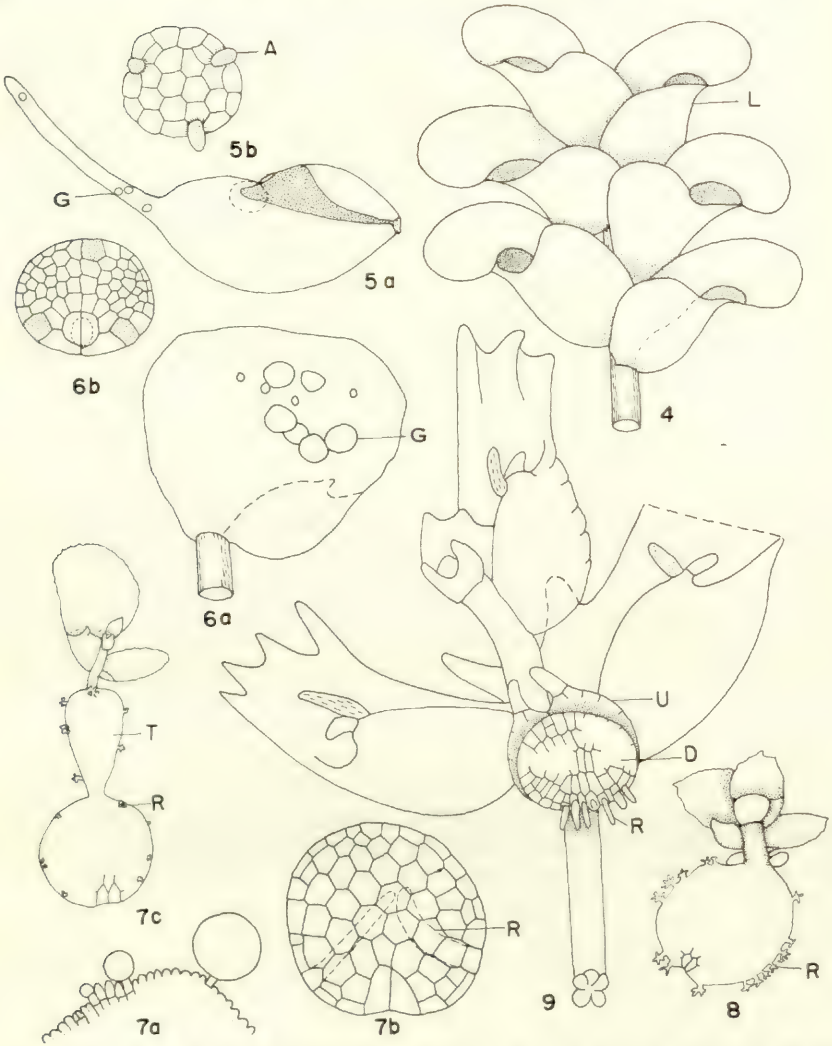
Still another highly specialized means of vegetative reproduction among the leaf-inhabiting species occurs in the very common *Drepanolejeunea inchoata*. The plants are relatively large, with broad, coarsely toothed leaves, and in addition to the branches with adult leaves, there are some with smaller leaves of the same sort, and some with very slender lanceolate leaves. These latter branches produce even smaller easily detached branches, the propagula. The propagulum (FIGURE 9) is a minute, slender branch with several leaves and underleaves. The first underleaf (FIGURE 9, U) is the largest and has, over much of its surface, a circular "suction disc" with slime secreting rhizoids from the marginal cells. This disc serves as an anchoring mechanism for the branchlet. Such propagula have been described by Evans (1902) for several Puerto Rican genera. In a study of epiphyllous hepatics of El Salvador, Winkler (1967) has also described the leaf-adaptions of many of these species.

Small-leaved microphyllous or flagelliform branches are developed in many species. In *Ceratolejeunea flagelliformis* (FIGURE 10 a *vs* 10 b) and *Prionolejeunea aemula* (FIGURE 13 a *vs* 13 b), the whole branch is readily detached and blown about, while in *Bazzania longistipula* (FIGURE 11 a *vs* 11 b) and *Calypogeia cellulosa* (FIGURE 12 a *vs* 12 b), the small-leaved branches are brittle and tend to break into short lengths. Both types form new plants and colonies in favorable surroundings.

Large numbers of fragments of leaves and stems are also to be found in any collection. In most species it has been demonstrated that the cells are totipotent and that new plants are produced in considerable numbers from such fragments, especially in such genera as *Bazzania*, *Plagiochila*, *Radula* and many genera of the Lejeuneaceae.

All of the above described methods of reproduction occur in abundance in the area of Pico del Oeste. This is indicated from the occurrence on the pollen-trap slides and the numbers of sporelings, gemmalings, specialized branches, and stem and leaf fragments found in our collections. They are carried by the wind, strong up- and down-drafts, and by driving rains. But these are examples of short-distance dispersals and it must be kept in mind that even on the four peaks of the Luquillo Mountains there is a considerable difference in the hepatic flora. How much of this difference is due to a matter of dispersal and how much to habitat diffierences is an open question, since the hepatics require only microhabitats within any area.

There is also a considerable difference in composition between the hepatic flora of Pico del Oeste and that at lower elevations, namely the Rain Forest, at 500 to 625 meters, or the several collecting localities at 700 to 750 meters.



FIGURES 4–9. Some leaf-inhabiting species. FIG. 4. *Colura clavigera*, showing the strongly inflated leaves (L), × 85. FIG. 5 a. *Cl. rhynchophora*, an inflated leaf with discoid gemmae (G), on the long-cylindrical tip, × 85. FIG. 5 b. A gemma with three attaching organs (A), × 240. FIG. 6 a. *Diplasiolejeunea unidentata*, leaf with discoid gemmae (G), × 60. FIG. 6 b. A gemma with three attaching organs, × 240. FIG. 7 a. *Cyclolejeunea accedens*, diagram of a portion of a leaf margin with discoid gemmae, × 60. FIG. 7 b. Gemma with two large attachment cells at its base, and a pair of long rhizoids (R) on the lower side. FIG. 7 c. Gemmaling, with the gemma below and the gemmothallus (T) with a leafy plant above. FIG. 8. *C. convexistipa*, gemma with short, branched, marginal rhizoids (R), and a young leafy plant. FIG. 9. *Drepanolejeunea inchoata*, a tiny propagulum with three leaves and two underleaves (U); the first underleaf bears a large "suction disc" with marginal rhizoids (R), which serve to attach the propagulum to a leaf, × 240. FIGURES 7 b, c, and 8 after Evans (1904).

There is evidence that certain of the species from these areas may have been repeatedly blown into the area of Pico del Oeste, but apparently they have not become established.

In any patch of hepatics here, there are one to several dominants and as many as 18 additional species, some of which are tiny fragments which have been caught in the tangled growth. No one of the collections contained only a single species. The fragments of stems with growing tips had two or three to a dozen leaves, often smaller or conspicuously reduced in size. The number of such stems which actually survive and grow into typical plants is not known.

In all, 95 collections of leafy Hepaticae were made on Pico del Oeste. Mr. Stotler examined all of the packets in great detail and made a permanent slide of each species in each packet, more than 650 slides in all. These include 15 families, 34 genera, and 62 species.

We wish to thank Drs. Carroll E. Wood and Richard A. Howard for collecting material (38 packets), and Dr. Howard for his hospitality, and for guiding us through the area. I also wish to thank the National Science Foundation for some financial aid. The specimens are housed at the University of Cincinnati.

In the following list an asterisk (*) denotes species reported from Puerto Rico for the first time. The numbers following each species indicate the number of times that species occurred in the total number of packets. In the distribution data "known" indicates that the data is taken from a monographic treatment of the genus, and "reported" indicates that the records are from the older literature and from lists.

TRICHOCOLEACEAE

Trichocolea flaccida (Spr.) Jack & Steph. 2/95.

With other hepatics on a tree trunk and on a leaf. Known from throughout the West Indies; Mexico, Guatemala; Colombia, Venezuela, Ecuador, Peru, Bolivia.

ISOTACHACEAE

Neesioscyphus bicuspidatus (Steph.) Grolle. 1/95.

Soil bank. Known from Puerto Rico, Guadeloupe, Martinique.

HERBERTACEAE

Herberta divergens (Steph.) Herzog. 20/95.

In tufts or pendent on trees and shrubs, and on leaves, including *Ocotea*, *Eugenia*, *Ilex*, and *Calyptranthes*, and on leaves of *Anthurium*. Known from Puerto Rico; Costa Rica; Brazil, Bolivia.

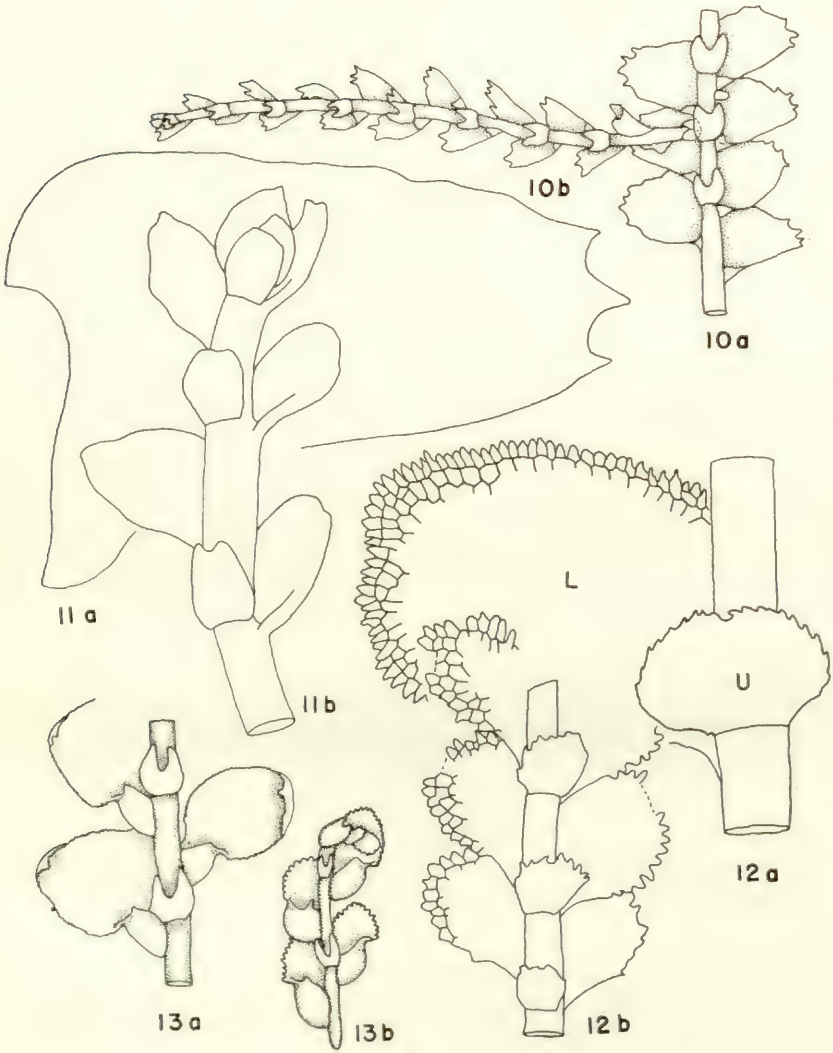
Herberta pensilis (T. Tayl.) Spr. 7/95.

In tufts or pendent on trees, shrubs, and leaves, including *Calyptranthes* and *Grammadenia*. Known from Cuba, Puerto Rico, Dominica; Costa Rica; Colombia, British Guiana, Brazil, Ecuador, Peru, Bolivia.

LEPIDOZIACEAE

Bazzania breuteliana (Lindenb. & Gott.) Trevis. 1/95.

A large "ball" on a tree trunk. Widespread in the West Indies, Central America, and the northern half of South America.



FIGURES 10–13. Some species with flagelliform or microphyllous branches. FIG. 10 a. *Ceratolejeunea flagelliformis*, adult stem, × 60. FIG. 10 b. Flagelliform branch of this species, × 60. FIG. 11 a. *Bazzania longistipula*, adult leaf, × 60. FIG. 11 b. Portion of a microphyllous branch of this species, × 60. FIG. 12 a. *Calypogeia cellulosa*, an adult leaf (L) and an underleaf (U), × 60. FIG. 12 b. Portion of a small-leaved branch of this species, × 60. FIG. 13 a. *Prionolejeunea aemula*, portion of an adult stem, × 60. FIG. 13 b. A short microphyllous branch of this species, × 60. Drawn from plants collected on Pico del Oeste.

Bazzania longa (Nees) Trevis. 27/95.
Abundant on tree trunks, twigs, and leaves, including *Tabebuia* and *Wallenia*, and on *Anthurium* and ferns. Known from Cuba, Jamaica, Puerto Rico, St. Kitts, Guadeloupe, Dominica, Martinique, and Trinidad. (Fragments of stems are common in many collections.)

Bazzania longistipula (Lindenb.) Trevis. 14/95.
In mats or deep tufts on tree trunks and branches, including *Eugenia*, *Ilex*, and *Miconia*. Known from throughout the West Indies, Central America, and tropical South America. (Fragments of stems are very common in collections in the mountains).

Bazzania roraimensis (Steph.) Fulf. 5/95.
Among other hepatics on trees. Known from Jamaica, Puerto Rico; Colombia, British Guiana, and Brazil. (All of the collections were depauperate fragments.)

Bazzania stolonifera (Sw.) Trevis. 1/95.
Forming a "ball" on a tree trunk. Common throughout tropical America.

Micropterygium carinatum (Grev.) Reim. 5/95.
With other hepatics on tree trunks and twigs. Known from Puerto Rico, Guadeloupe, Dominica, Martinique; Venezuela.

Lepidozia patens. Lindenb. 16/95.
In deep tufts on trunks and branches of trees and shrubs, including *Eugenia*, *Ocotea*, *Tabebuia*, and *Wallenia*. Known from Cuba, Jamaica, Haiti, Puerto Rico, St. Kitts, Guadeloupe, Dominica, Martinique; Guatemala; Colombia, Venezuela.

Telaranea sejuncta (Ångstr.) S. Arnell. 1/95.
Decayed log. Known from coastal eastern United States; Puerto Rico, Guadeloupe, Dominica; Mexico, Guatemala, Costa Rica, Honduras; Colombia, Venezuela, Brazil, Ecuador, Peru, Bolivia.

CALYPOGEIACEAE

Calypogeia cellulosa (Spreng.) Steph. 11/95.
Mats or among other hepatics on tree trunks and branches, leaves and over ferns. Known from Cuba, Puerto Rico, Guadeloupe, and Dominica.

Calypogeia elliottii Steph. 4/95.
In mats on tree branches, tree base, and old leaves. Known from Puerto Rico, Dominica.

Calypogeia peruviana Nees & Mont. 1/95.
On leaf of *Anthurium*. Widespread and abundant throughout tropical America. (It most commonly grows on moist banks and rocks, logs, and tree bark.)

CEPHALOZIACEAE

Cephalozia caribbeania Fulf. 1/95.
On bark, tree base. Known from Cuba, Jamaica, Puerto Rico, Guadeloupe, Dominica, Trinidad; Mexico, Guatemala, Honduras; Venezuela.

**Nowellia caribbeania* Fulf. 1/95.
On mound on bark of tree. Known from Puerto Rico; Guatemala, Honduras, Costa Rica; Venezuela.

Nowellia dominicensis Steph. 2/95. (*N. bicornis* (Spr.) Fulf.)
Among tufts of other hepatics. Known from Puerto Rico, Guadeloupe, Dominica.

ODONTOSCHISMACEAE

Alobiellopsis dominicensis (Spr.) Fulf. 1/95.
On compact soil along path. Known from Puerto Rico, Dominica, Martinique, Trinidad.

Odontoschisma prostratum (Sw.) Trevis. 1/95.
Near the base of a tree trunk. Known from eastern United States; Cuba, Jamaica, Puerto Rico, Guadeloupe, Martinique.

ZOOPSIDACEAE

Zoopsis antillana Steph. 1/95.
Among other hepatics on a tree trunk. Known from Cuba, Puerto Rico, Dominica, Trinidad.

LOPHOCOLEACEAE

Heteroscyphus elliottii (Steph.) Pagán 1/95.
Loose mat on a tree branch. Reported from Puerto Rico, Dominica.

Leptoscyphus gibbosus (T. Tayl.) Mitt. 4/95.
In mats on tree bark, occasionally on the ground. Known from Puerto Rico, Guadeloupe, Martinique.

LOPHOZIACEAE

Syzygiella perfoliata (Sw.) Spruce. 5/95.
In tufts on bark and leaves or hanging from tree branches. Known from Jamaica, Puerto Rico; Costa Rica; Brazil, Peru. (Most of the stems have most leaves conspicuously bifid.)

PLAGIOCHILACEAE

Plagiochila bidens Gott. 20/95.
On tree bark and living leaves including *Calyptranthes*, *Grammadenia*, *Micropholis*, *Ocotea*, *Trichilia*. Reported from Cuba, Puerto Rico, Dominica, Guadeloupe; Bolivia.

Plagiochila bursata (Desv.) Lindenb. 6/95.
Reported common in the mountains of the American tropics.

Plagiochila chinantlana Gott. 22/95.
On tree bark and leaves. Reported from Puerto Rico; Mexico, Costa Rica; Colombia, Peru.

plagiochila dominicensis T. Tayl. 6/95.
In large loose tufts on trees and over ferns. Reported from Cuba, Puerto Rico, Dominica; Mexico; Colombia, Venezuela.

**Plagiochila jamaicensis* Lindenb. & Hpe. 5/95.
On twigs and branches. Reported from Jamaica, Puerto Rico.

Plagiochila rutilans Lindenb. 1/95.
On trees. Reported from Cuba, Puerto Rico, Guadeloupe, Dominica, Trinidad; Costa Rica; Venezuela, British Guiana, Brazil.

**Plagiochila subbidentata* T. Tayl. 4/95.
On bark and leaves of trees and shrubs. Reported from Jamaica, Puerto Rico.

[2] **Adelanthus brevicaulis* Steph. 13/95.

[2] Not much information is available as to the nature of the shoot/sporophyte relationship or the characteristics of the sporophyte in this species. I have tentatively placed it in this family.

On trunks, branches and leaves of trees and shrubs, including *Grammadenia*, *Ocotea*, *Tabebuia*, *Wallenia*. Reported from Puerto Rico, Guadeloupe; the Andes.

SCAPANIACEAE

Scapania portoricensis Hpe. & Gott. 3/95.

On soil bank, and among other hepatics on tree bases and branches. Reported from Cuba, Jamaica, Puerto Rico; Colombia, Venezuela, Brazil, Ecuador.

RADULACEAE

Radula fendleri Gott. ex Steph. 5/95.

In mats and tufts on leaves and branches. Known from Puerto Rico, Guadeloupe, Martinique, Surinam, Venezuela.

Radula saccatiloba Steph. 15/95.

In tufts and mats on tree trunks, branches, and leaves including *Calyptranthes*, *Ocotea*, *Tabebuia*, and over ferns. Known from Cuba, Jamaica, Puerto Rico, Guadeloupe, Dominica, Martinique.

FRULLANIACEAE

**Frullania subtilissima* (Nees & Mont.) Lindenb. 6/95.

In mats on twigs and living leaves, including *Ilex* and *Micropholis*. Reported from Dominican Republic, Puerto Rico, Guadeloupe, Dominica; French Guiana, Brazil.

LEJEUNEACEAE

Ceratolejeunea flagelliformis (Steph.) Fulf. 6/95.

On bark of trees, shrubs, and on living leaves. Known from Puerto Rico, Martinique; Costa Rica. (Detached flagelliform branches are frequent.)

Ceratolejeunea maritima (Spr.) Steph. 9/95.

On bark of trees and shrubs, living leaves, and over ferns. Common throughout tropical America.

Ceratolejeunea patentissima (Hpe. & Gott.) Evans 16/95.

In mats on living leaves including *Ardisia*, *Calyptranthes*, *Ilex*, *Micropholis*. (Most of the collections belong to var. *acutifolia* Fulf., with acute leaves.) Known from Cuba, Jamaica, Puerto Rico, Guadeloupe, Martinique; Colombia, Venezuela.

Ceratolejeunea valida Evans. 45/95.

On bushes, twigs, and living leaves. Known only from Puerto Rico.

**Colura clavigera* (Gott.) Jovet-Ast. 1/95.

With other hepatics, on bark. Known from Puerto Rico, Guadeloupe.

Colura rhynchophora S. Jovet-Ast. 18/95.

On leaves including, *Guzmania* and *Vriesia*, or as short stems among other hepatics. Known from Puerto Rico, Guadeloupe.

Cyclolejeunea accedens (Gott.) Evans. 17/95.

On living leaves, more rarely as fragments among other bryophytes. Known from Puerto Rico, St. Kitts, Guadeloupe, Dominica, St. Vincent; Venezuela, Peru, Bolivia.

Cyclolejeunea convexistipa (Lehm. & Lindenb.) Evans 16/95.

On living leaves, rarely on bark, often fragments mixed with other hepatics. Both species reproduce by large, unistratose, discoid gemmae which are of frequent occurrence on leaves. Widely distributed in tropical America.

Cystolejeunea lineata (Lehm. & Lindenb.) Evans. 41/95.
On trees, often in festoons, on banks among other hepatics. Known from Puerto Rico, St. Kitts, Guadeloupe, Dominica, Martinique, St. Vincent; Colombia, French Guiana, Brazil.

Diplasiolejeunea unidentata (Lehm. & Lindenb.) Schiffn. 11/95.
Mats on leaves and twigs, including *Ilex*, *Miconia*, *Trichilia*. Known from Jamaica, Puerto Rico, Guadeloupe, Dominica, Martinique, St. Vincent; El Salvador. The species produces abundant unistratose, discoid gemmae on the leaves.

Drepanolejeunea anoplantha (Spr.) Steph. (*D. subulata* Steph.) 15/95.
On living leaves but more characteristically as small stems among other hepatics. Known from Cuba, Jamaica, Puerto Rico, St. Kitts, Guadeloupe; Venezuela, Brazil, Peru.

Drepanolejeunea crucianella (T. Tayl.) Evans. 1/95.
On leaves. Widespread in tropical America.

Drepanolejeunea evansii Bischl. (*D. infundibulata* (Spr.) Evans) 1/95.
On leaves. Known from Puerto Rico, Guadeloupe, Martinique.

Drepanolejeunea inchoata (Meissn.) Steph. 29/95.
On leaves and mixed with other hepatics. Widespread throughout tropical America. This species and probably others in this genus produce very specialized short branches for vegetative reproduction.

Drepanolejeunea fragilis Bischl. (*D. araucariae* Evans). 17/95.
On leaves and as fragments among other hepatics. Known from Jamaica, Puerto Rico, Guadeloupe; Guatemala, Costa Rica; Colombia, Surinam, Brazil.

Harpalejeunea heterodonta Evans. 12/95.
On leaves and as fragments among other hepatics. Known from Puerto Rico, Guadeloupe, Martinique; Colombia, British Guiana.

Harpalejeunea uncinata Steph. 13/95.
On bark and leaves and as fragments among other hepatics. Known from Cuba, Dominican Republic, Puerto Rico, Guadeloupe, Martinique, Trinidad; Panama.

Neurolejeunea breutelii (Gott.) Evans 1/95.
On a leaf. Known throughout tropical America.

Prionolejeunea aemula (Gott.) Evans. 19/95.
On leaves and among other hepatics. Known from Puerto Rico, St. Kitts, Guadeloupe, Dominica; Colombia, Ecuador, Peru. Small branches with smaller leaves are readily detached and are frequent among other hepatics.

Prionolejeunea aequitexta Evans. 1/95.
On living leaves. Known from Puerto Rico.

Prionolejeunea exauriculata Evans. 1/95.
On a living leaf. Known from Puerto Rico.

Prionolejeunea innovata Evans. 3/95.
In small mats on twigs, with other hepatics. Known from Puerto Rico.

Rectolejeunea phyllobola (Nees & Mont.) Evans. 1/95.
On a leaf. Southern Florida, widely distributed in the West Indies; Mexico, Costa Rica.

**Strepsilejeunea involuta* Steph. 3/95.
On bark and leaves. Reported from Puerto Rico, Dominica, St. Vincent; Brazil.

Taxilejeunea sulphurea Spr. 4/95.
In loose tufts or pendent on trees and leaves, and over banks and logs. Widespread in tropical America.

Trachylejeunea inflexa Steph. 21/95.
In mats and tufts on trees and among other hepatics. Said to be common in the American tropics.

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TYPES OF BLIND VEIN-ENDINGS IN THE DICHOTOMOUS VENATION OF CIRCAEASTER

ADRIANCE S. FOSTER

A SALIENT FEATURE of the predominantly reticulate venation patterns of many dicotyledons as well as certain monocotyledons is the presence of blind vein-endings within the numerous areoles of the vascular system. Pray (1963) has treated in great detail the morphology and histogenesis of such vascular terminations in the leaves of *Liriodendron*, *Aucuba*, and *Smilax*. He concluded that "it seems probable that development of the minor venation of all angiosperms which have reticulate patterns similar to those investigated here involves similar ontogenetic processes."

In the highly contrasted dichotomous venation patterns of *Kingdonia* and *Circaeaster*, however, the majority of the ultimate veinlets terminate in marginal teeth, vein anastomoses are infrequent and when areoles are formed, they are devoid of included vein-endings (Foster 1959, 1963, 1966, 1968; Foster & Arnott 1960). In describing this type of venation, I used the expression "blind vein-endings" to designate those veinlets which terminate in various positions and levels without reference to any of the distal marginal teeth. Do such blind vein-endings represent the vascular supply of "arrested" marginal teeth, or should they be considered as "supplementary veins" which are characteristic of "open" dichotomous venation in general?

The present article describes and seeks to interpret morphologically the various types of blind vein-endings encountered in my extensive surveys of cultivated plants of *Circaeaster agrestis* Maxim. My original investigation of herbarium material revealed very few examples of blind vein-endings, although it was admitted that their apparent rarity might have been the result of insufficient leaf sampling (Foster 1963, pp. 310, 311). In the leaves obtained from successive populations of *Circaeaster* raised in the growth chamber and in the Botanical Garden of the University of California during the past four years, however, blind vein-endings were relatively frequent. Not only were unbranched marginal and central endings found, comparable to some of those previously described, but a totally unexpected type of marginal, blind, dichotomously branched ending was discovered. This novel aspect of the venation of *Circaeaster* has been very carefully studied and constitutes a point of particular emphasis in the present paper.

MATERIALS AND METHODS

Ripe fruits, collected from the 1967 population of cultivated plants, were sown in large pots and 128 plants were raised from seedlings to maturity,

in a growth chamber in which a photoperiod of 16 hours and a constant temperature of 50° F. were maintained. This temperature, which was about 10° higher than that employed in previous years, appeared to be a very significant factor in the unusually vigorous growth of the 1968 plants.

At maturity, the plants were harvested and the leaf-rosettes preserved in 70% alcohol. A total of 6,179 leaves (including the larger floral bracts) were dissected from these specimens, examined for anastomoses and blind vein-endings, and the data recorded in tabular form. Leaves which were selected as the basis for the illustrations in this paper were cleared in NaOH followed by concentrated chloral hydrate, thoroughly dehydrated in the alcohol-series, and stained in a 1% solution of safranin in equal parts of absolute alcohol-xylene. Some of the leaves however were very difficult to clear satisfactorily in low concentrations of NaOH (i.e., 2.5%–5%) because of peculiar "amorphous" inclusions in many of the parenchyma and epidermal cells. Prolonged treatment in cold 10% NaOH (for 3 weeks or longer) followed by chloral hydrate in most instances improved the appearance of such leaves prior to staining. In order to secure evenly stained preparations for subsequent photography, the leaf-specimens were left in the safranin for a relatively short period, approximately 1½ to 2 hours rather than overnight as in the case of most of the leaves processed in previous years. This shorter period in the stain gave excellent preparations, especially when the destaining was done in a mixture of 3 parts of xylene to 1 part of absolute alcohol. This solution prevented the too rapid leaching of safranin which always tends to occur when a mixture of equal parts of xylene-alcohol is used for destaining.

I am grateful to Mrs. Irene Baker for her invaluable assistance in dealing with the germination and culture of the plants in the growth chamber. Thanks are also due Mr. Alfred A. Blaker, who made the photomicrographs, and Mrs. Emily E. Reid for preparing and arranging the line drawings. I am also very appreciative of my wife's assistance in proof-reading the manuscript.

Symmetrical Patterns of Dichotomous Venation

Comprehensive surveys of leaf morphology in herbarium collections and cultivated plants of *Circaeaster* have clearly shown the considerable fluctuation in (a) the shape of the lamina, (b) the number of teeth at the distal margin, and (c) the degree of symmetry of the venation patterns (Foster 1963, 1966, 1968). In many of the leaves obtained from herbarium material, the lamina is flabelliform or broadly ovate in contrast to the frequently narrower obovate or spatulate contour of the leaf-blade developed in the various populations of cultivated plants. Despite the variation in form and symmetry of the lamina, however, it is evident that usually all the vein-endings in a given leaf terminate in corresponding marginal teeth. This type of one-to-one correlation tends to predominate regardless of whether an even or an odd number of marginal teeth is present. It is,

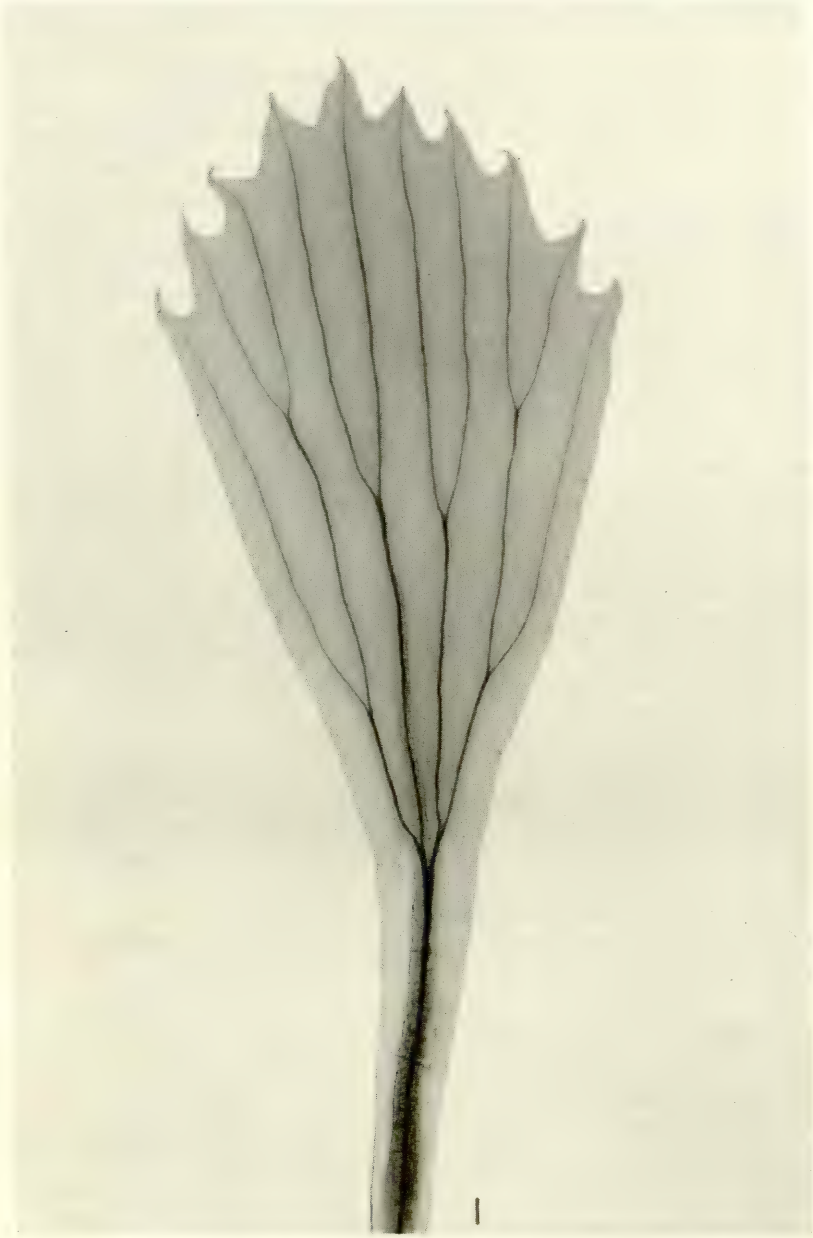

FIG. 1. Cleared leaf with symmetrical open dichotomous venation. Bifurcation of the petiolar bundle at base of lamina yields two "identical" types of vein-systems, each composed of five veinlets terminating in corresponding marginal teeth, × 8.6.

however, particularly striking in those cases where the associated pattern of dichotomous venation is symmetrical (Foster 1963, *Pl. I, fig. 5*).

An unusually clear example of "isotomous" venation is shown in FIGURE 1. In this leaf, the bifurcation of the petiolar bundle is followed by the dichotomy of each branch, resulting in two symmetrical pairs of veins at the base of the lamina. From each pair of basal veins, by appropriate dichotomy at successive and approximately opposite levels, two "identical" systems of veins are produced. Each system consists of a long unbranched marginal strand and two pairs of additional veins *all* of which enter corresponding marginal teeth. The two halves or "sectors" of the lamina are thus vascularized by corresponding vein-systems which are separated from each other by a long, well defined "neutral space." This term was used by Bock (1962, pp. 9 and 10, *Figs. 15, 17*) to designate the non-vascularized area between two vein-systems in leaves with symmetrical dichotomous venation. In this connection, the basic morphological resemblance between the venation pattern shown in FIGURE 1 and that of the leaf of *Ginkgo* and a pinnule of *Adiantum* is indeed remarkable (see Bock 1962, *Fig. 13a, b*).

Unbranched Blind Vein-endings

Blind vein-endings in the leaves of *Circaeaster* may be conveniently classified into two main "types" viz.: branched and unbranched. The first type, to be described later, is relatively infrequent and has only been observed in a few leaves of cultivated plants (FIGS. 16–22, 29). In contrast, unbranched blind endings are rather commonly seen and occur in a great many leaves of the plants which were raised in the growth chamber during 1968 (FIG. 2).

It must be emphasized in the first place that the presence or absence of blind vein-endings is obviously not correlated with the size or shape of a leaf or its relative position in the leaf-rosette. Comparatively small primary leaves with only a few teeth may develop one or more blind endings (FIG. 3) and similar endings may occur in floral bracts (FIG. 4) and larger foliage leaves (FIGS. 5–8).

With reference to their general position in the venation pattern, unbranched vein-endings apparently occur most commonly in the lateral marginal region of the lamina. In some cases there is only a single blind ending in a leaf (FIGS. 4, 6, 7, 8, 10) but a number of examples have been found where a blind ending is present in each margin of the lamina (FIGS. 3, 5, 11). Considerable variation exists with respect to the level of divergence and the relative length of unbranched marginal blind endings. Often the ending is very short and diverges at a relatively high level in the lamina (FIG. 2, at right). But a good many examples have been found of marginal endings which diverge at the very base of the lamina. In these cases the marginal veins may terminate blindly after extending only a short distance along the margin (FIGS. 3, 5). In other leaves, however, the blind ending may be more highly developed and extend nearly the full length of the lateral margin (FIGS. 10, 11). Marginal blind endings, more or less inter-

mediate in length between these extremes also occur and are shown at the left of FIGURES 7 and 8.

Less frequently, unbranched blind vein-endings occur in the upper central region or even in the distal margin of the lamina. In certain leaves which were studied, blind vein-endings are restricted to the central portion of the lamina (FIG. 13), while in others, both marginal and central blind endings occur in the same lamina (FIGS. 2, 12, 14). One of the most remarkable examples I have seen of a distal blind vein-ending is represented in FIGURE 15. In this leaf, the short acroscopic branch of a very symmetrical vein-dichotomy ends blindly, as shown by the arrow, *between* two adjacent teeth. It is also evident that central blind endings, as represented in FIGURES 2, 13, 14, commonly terminate at varying distances *below* the narrow sinuses between adjacent marginal teeth.

During the course of this investigation a very careful search was made to discover whether the development of unbranched blind vein-endings was ever correlated with the presence of corresponding vestigial marginal teeth. *A priori* it might be anticipated that since the sister-branch of a marginal or central blind ending enters a corresponding tooth, or by further dichotomous branching vascularizes several successive teeth, the blind ending itself might represent the vascular supply of an undeveloped or rudimentary tooth. But only a single possible correlation of this sort was encountered (FIGS. 6, 9). However, the peculiar massive cluster of tracheary elements found at the base of this vestigial tooth raises certain problems which will be more appropriately considered later in the discussion section of this paper.

Marginal Blind Dichotoms

As mentioned in the introduction of this paper, one of the most unexpected results of my venation survey was the discovery of a dichotomously branched type of blind vein-ending in the lateral margin of the lamina of certain leaves (FIGS. 16–22). In order to relate such ramified endings to the overall pattern of dichotomous venation in *Circaeaster*, I have adopted Bock's (1962) term "dichotom." This term, which is brief and convenient for descriptive purposes is defined by Bock (1962, p. 6, *Fig. 1*) as follows: "As a general principle, *dichotomy* should be considered a growth pattern in which a base member develops two branch members, both advancing in a direction different from that of the base member. . . . The two angles formed by the base and the two branches may be equal, but also may vary. They are called the base angles, being always paired, while the angle formed by the two branches is the branch angle. Such a single dichotomy is called a *dichotom*."

In applying Bock's general concept to the venation patterns shown in FIGURES 16 to 22, the following interesting morphological differences between the various forms of marginal blind dichotoms are quite evident, viz:

1. POINT OF ORIGIN OF THE BLIND DICHOTOM. In the leaves depicted in FIGURES 19 and 22, the "base member" of the dichotom is a relatively long

major lateral vein which bifurcates in the lower marginal region of the lamina. In contrast, the "base member" of the blind dichotom in the other five leaves represents the *outer branch of a lateral vein-dichotomy* which originates near the lamina base. In each of these cases, the sister-branch of the blind dichotom, by means of further dichotomous branching, forms two or three vein-endings which vascularize corresponding lamina teeth (FIGS. 16, 17, 18, 20, 21).

2. LENGTH AND SYMMETRY OF DICHOTOM-BRANCHES. In one of the leaves, the two "branch members" of the dichotom are extremely symmetrical and approximately equal in length (FIGS. 18, 25). But in all the other examples, the *inner* (i.e. submarginal) "branch member" is more or less conspicuously longer than its sister-branch. This remarkable asymmetry is obvious in dichotoms with relatively short branches (FIGS. 16, 19, 20, 24, 26) but is particularly striking when the inner branch terminates near the dentate margin of the lamina (FIGS. 17, 21, 22, 23).

3. MODE OF TERMINATION OF DICHOTOM-BRANCHES. As in the case of unbranched vein-endings, close attention was given to the possible association of blind dichotoms with corresponding rudimentary marginal teeth. Careful study of the venation under high magnification showed that in six of the leaves, the terminal tracheary elements of the dichotom-branches end freely in the mesophyll and that no histological evidence exists of vestigial teeth above such endings (FIGS. 23, 24, 26). In one leaf, however, as shown in detail in FIGURE 25, a peculiar "shelf-like" projection of the lamina margin lies directly above the outer branch of the blind dichotom. Whether this "shelf" should be regarded as a "rudimentary tooth" is extremely problematical. When the projection was carefully examined under higher magnification than is represented in FIGURE 25, it was found completely devoid of tracheary elements and in this respect quite unlike the apparently "authentic" vestigial tooth shown in FIGURE 9.

DISCUSSION

The varied types of blind vein-endings which have just been described, collectively represent a puzzling aspect of the dichotomous venation pattern of *Circaeaster*. Since usually all the vein-endings in a given leaf enter corresponding marginal teeth, the blind endings which may additionally occur in various regions of the lamina pose interesting morphological and ontogenetic questions.

From the standpoint of a morphological analysis of the *mature venation*, an unbranched blind ending in most instances appears to represent the shorter and usually less well-developed branch of a typical vein-dichotomy. In the simplest case the "dichotom" which yields a blind ending is very symmetrical in organization, one of its branches entering a marginal tooth, the other terminating at various levels in the lateral margin of the lamina (FIGS. 2, 11, at right). More complex patterns result when the sister-branch of the blind ending forks once or twice, forming terminal veinlets which enter two or three adjacent teeth (e.g. FIGS. 4, 7, 8, 10). Comparable

variations in venation pattern and in the degree of development of the blind ending also occur in the central or distal portions of the lamina (FIGS. 2, 12–15).

It is tempting, in the case of unbranched blind vein-endings, to speculate that they may represent the *persistence* of the vascular supply of "suppressed" marginal teeth. The present investigation, however, gives little real support to such an assumption.

In the first place, the majority of the marginal blind endings are more or less strictly parallel with the edge of the lamina and terminate without reference to any protuberance which would qualify as the "rudiment" of a tooth (FIGS. 2, 4, 5, 7, 8, 10, 11). Only one leaf was encountered in my entire survey in which a diminutive tooth is situated *above* the tip of a long marginal blind ending. (FIG. 6). However, since the longitudinal course of differentiation of xylem in the veins entering "normal" leaf teeth has not been determined, the significance of the *isolated* cluster of tracheary elements at the base of this vestigial tooth remains obscure (FIG. 9). Such an irregular and exaggerated development of the primary xylem does not occur, for example, at the point of entrance of a vein into a well developed tooth, nor is it matched in those puzzling cases where a tooth is vascularized by a basally unconnected strand (FIG. 19, right margin).

Secondly, some of the vein-endings terminate very near the branch of a vein-dichotomy, suggesting that they may represent the incomplete development of Type V anastomoses rather than the vascular supply of "arrested" teeth (FIG. 11, at left margin; FIG. 12, upper center). A further example of this interesting condition has already been described in a recent paper on anastomoses in *Circaeaster* (Foster 1968, p. 61 and *Fig. 15*).

Most of the objections which have just been raised against interpreting unbranched blind endings as the vascular supply of "arrested" teeth are also valid with respect to the morphological nature of marginal blind dichotoms (FIGS. 16–22, 29). In the comparatively few leaves which had formed such ramified endings, there was no evidence of paired vestigial teeth and only one instance, as shown in FIGURE 25, of a peculiar shelf-like extension of the margin above the dichotom. This "shelf," however, lacks vasculature and does not seem to qualify as a rudimentary tooth; its morphological "significance," if any, is highly problematical.

From a comparative viewpoint it is important to note the occurrence of blind vein-endings in the dichotomous venation of other plants. *Kingdonia* is a good example for comparison because of the abundance and consistent development of blind endings in the dichotomously veined segments of its relatively large lamina (Foster 1959, Foster & Arnott 1960). Although the majority of the terminal veinlets enter corresponding marginal teeth, as in the smaller lamina of *Circaeaster*, 14.2% of all vein-endings studied in *Kingdonia* terminated blindly at various levels and positions in the lamina segments. Very commonly, the blind ending reaches the side or base of the sinus which separates adjacent marginal teeth (Foster & Arnott 1960, *Fig. 14*). But one of the most interesting points of similarity between *Circaeaster* and *Kingdonia* is the occurrence in both genera of marginal

blind dichotoms. FIGURE 27 represents the enlargement of a small part of the margin of a lamina segment of *Kingdonia*. The branches of the conspicuous blind dichotom shown in this figure are unequal and, as in *Circaeaster*, the inner branch is much longer than the outer (compare FIG. 27 with FIGS. 22 and 23). It is also notable that each of the lateral veins of the small tepals of the flower of *Kingdonia* may dichotomize and form two unequal freely terminating branches very much like the branching pattern of some of the marginal dichotoms of *Circaeaster* (Foster 1961, p. 402, *Figs. 4a, 5*).

When one seeks for additional examples of blind vein-endings in dichotomous venation patterns, the genus *Adiantum* comes to mind as worthy of study. In *A. capillus-veneris* L. the great majority of the vein-endings extend into corresponding marginal teeth, as in *Circaeaster*, and blind-endings are apparently rare in occurrence (Knobloch & Correll 1962, *Plate 13, Fig. 1*). My own extremely limited investigations on *A. cooperi* Baker, a species native to Costa Rica, revealed striking examples of marginal blind dichotoms, very similar to those in the leaves of *Circaeaster* and *Kingdonia* (FIG. 28). This is clearly a remarkable example of parallel evolution, comparable to the similarity between the types of vein-anastomoses in *Circaeaster* and those in such unrelated taxa as *Anemia*, *Zamia* and *Ginkgo* (Foster 1968, pp. 63–65). In this connection, it is of interest to note that Arnott (1959, p. 408 and *Fig. 9*), in his intensive study of dichotomous venation in *Ginkgo*, found examples of "veins ending a considerable distance from the margin." Such veins seem entirely comparable to the central blind endings which may develop in *Circaeaster* (compare Arnott's *Fig. 9* with FIGS. 2 and 13 of the present paper).

In conclusion, the need for thorough ontogenetic studies on the time of origin and mode of differentiation of blind vein-endings in dichotomous vasculature should be strongly emphasized. It would certainly be of morphological interest, in the case of *Circaeaster*, for example, to know (1) how strictly the initiation and development of marginal teeth is *coordinated* with the *pattern of differentiation* of dichotomous venation and (2) the time of origin and the longitudinal course of development of the various types of blind vein-endings. Whether detailed information on these problems would also shed light on the phylogenetic significance of dichotomous venation in *Circaeaster* remains, however, in my opinion, a completely open question.

[*Postscript to original manuscript*]

After the manuscript of the present paper had been completed, a remarkable type of marginal blind dichotom was found in which the *outer*, rather than the inner branch, was conspicuously longer than its sister branch (FIGURE 29). Whether this type of asymmetrical vein dichotomy is "exceptional" or is as frequent in occurrence as the marginal dichotoms illustrated in FIGURES 16–26 of this paper, remains to be determined by further surveys of leaf venation in *Circaeaster*.

FIGURE 29. Leaf with conspicuous asymmetrical blind dichotom which represents the bifurcation of the basal vein at the *left* of the lamina. Note that the basal vein at the *right* has formed three veinlets which terminate in corresponding teeth at the distal margin of the lamina. The scale at the side of the drawing equals 1 mm.

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EXPLANATION OF PLATES

PLATE I

FIG. 2. Leaf with two blind vein-endings, one in upper central region of lamina, the other in the margin at right. Note that the petiolar bundle dichotomizes far below the lamina-base, forming two asymmetrical vein-systems, × 15.8.

PLATE II

FIGS. 3–8. Leaves with marginal blind vein-endings. FIG. 3. Primary leaf with a blind vein-ending at each margin. FIG. 4. Floral bract with relatively long blind ending at right margin. FIG. 5. Leaf with eight symmetrically-vascularized teeth and a blind vein-ending at each margin. Note particularly the very low level of divergence of the blind ending at right. FIG. 6. Leaf with long blind vein-ending and very rudimentary tooth (indicated by arrow) at left margin. The structural details of the cluster of tracheary elements found at base of this tooth are shown in FIG. 9. FIG. 7. Leaf with eight symmetrically-aligned teeth and an unbranched vein-ending at left margin. FIG. 8. Leaf with two well-defined vein systems, the one at left with a long marginal blind ending. Note also vein-approximation at lower left of lamina. The scale at the side of each drawing equals 1 mm.

PLATE III

FIG. 9. Highly magnified view of the cluster of tracheary elements at the base of the vestigial lateral tooth of the leaf shown in FIG. 6, × 250.

PLATE IV

FIGS. 10–15. Leaves illustrating diversity in position and number of blind endings. FIG. 10. Leaf with ten symmetrically vascularized teeth and a long blind ending at left margin. FIG. 11. Leaf with eight symmetrically aligned teeth and two marginal blind vein-endings. FIG. 12. A leaf with two blind endings, one in central region of lamina, the other at the right margin. FIG. 13. Leaf with two unequal blind vein-endings, both in upper central portion of lamina. FIG. 14. Asymmetrical lamina with three blind endings, one at left margin, the other two in upper central area. FIG. 15. Leaf with asymmetrical lamina showing two blind vein-endings, one very short and rudimentary in upper central region, the other, indicated by arrow, terminating *between* two teeth at left. Note conspicuous Type I anastomosis in this leaf and short unconnected xylem strand (represented as a short isolated black line near distal margin of lamina). The scale at the side of each drawing equals 1 mm.

PLATE V

FIGS. 16–22. Leaves illustrating marginal blind dichotoms. FIG. 16. Dichotom, at left margin, with nearly equal branches. Details shown in FIG. 24. FIG. 17. Dichotom, at right margin, with unequal branches, the longer terminating below vascularized tooth. See FIG. 23 for details. FIG. 18. Leaf with very symmetrical blind dichotom at left margin. See FIG. 25 for details. FIG. 19. Dichotom, at left margin, with unequal branches represented in more detail in FIG. 26. Note that outermost tooth at right is vascularized by an unconnected strand (*US*). FIG. 20. Leaf with an unusual combination of an unbranched blind-ending at right margin and a symmetrical blind dichotom at left margin of lamina. FIG. 21. Dichotom, with unequal branches, at left margin of lamina. FIG. 22. Dichotom, at right margin of lamina, with conspicuously unequal branches. This leaf and the one shown in FIG. 7 are from the same plant. The scale at the side of each drawing equals 1 mm.

PLATE VI

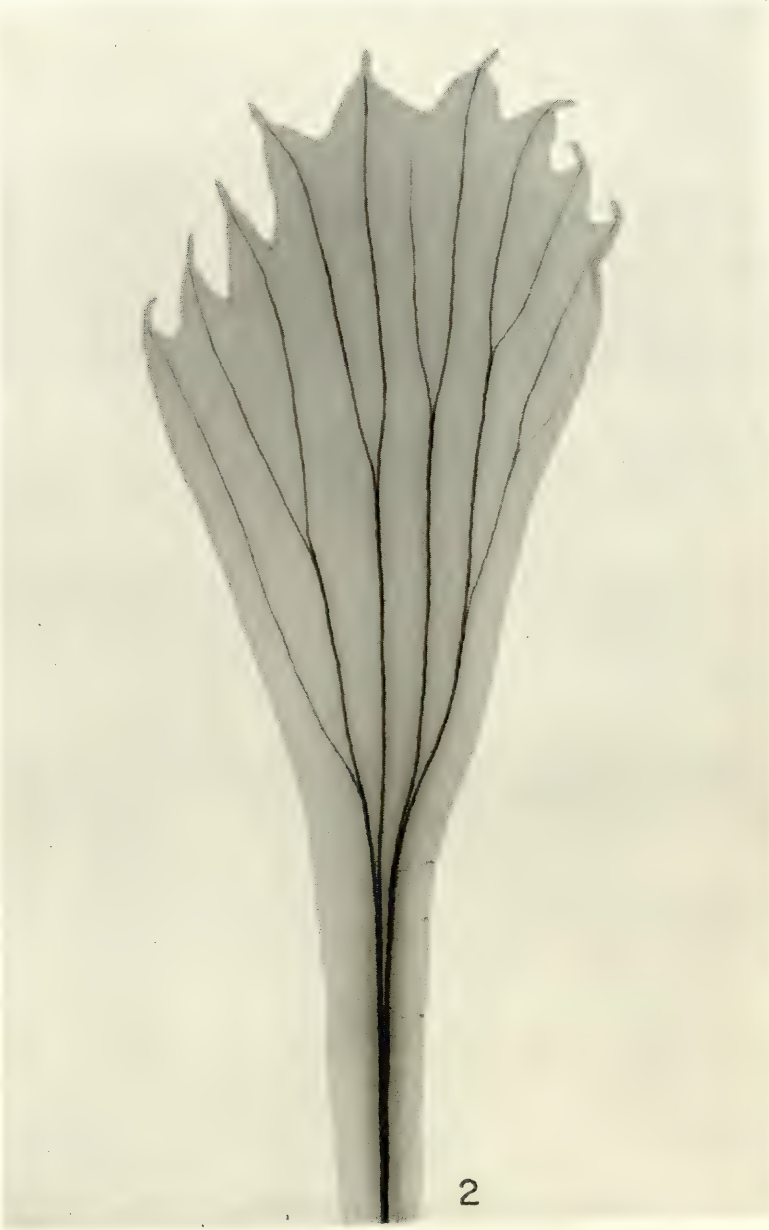
Marginal blind dichotoms. FIG. 23. Structural details of dichotom of leaf shown in FIG. 17, × 49. FIG. 24. Magnified view of dichotom of leaf represented in Fig. 16, × 40.

PLATE VII

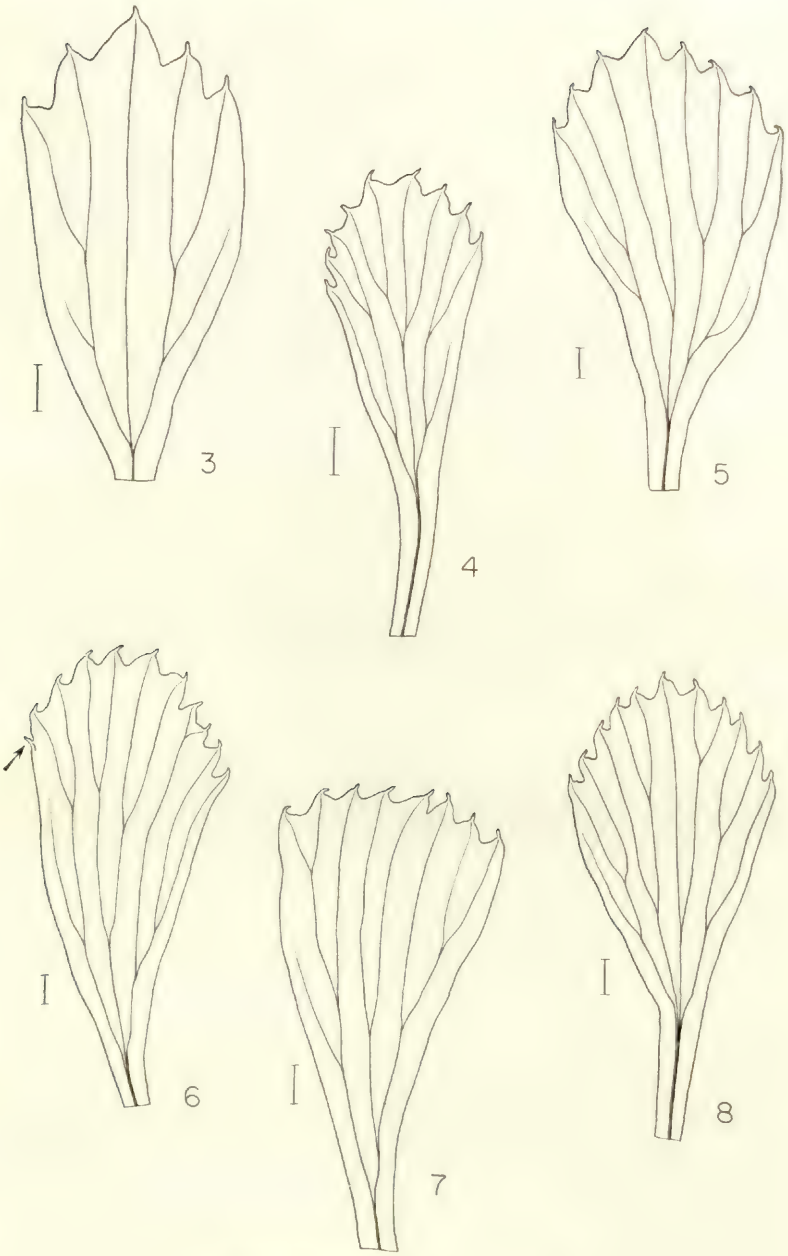
Marginal blind dichotoms. FIG. 25. Structural details of the very symmetrical marginal dichotom of the leaf shown in FIG. 18. Note that the dichotom terminates a short distance below a shelf-like projection of the lamina-margin, × 54. FIG. 26. Greatly enlarged view of dichotom of leaf represented in FIG. 19, × 67.

PLATE VIII

FIG. 27. Portion of marginal region of lamina segment of *Kingdonia uniflora* showing blind dichotom similar in type to that in leaf of *Circaeaster*, represented in FIG. 23, × 15.5. FIG. 28. Marginal region of pinnule of *Adiantum cooperi*, showing at lower left, a blind dichotom. Note remarkable similarity to blind dichotoms of *Circaeaster* shown in FIGS. 17, 19, and 22, × 15.5.

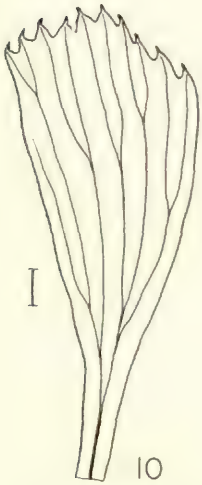


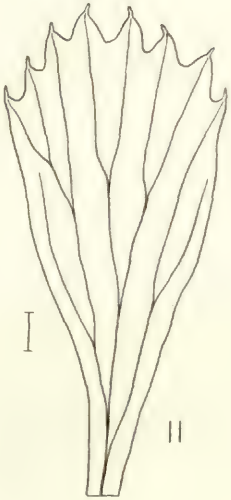
FOSTER, VENATION IN CIRCAEASTER

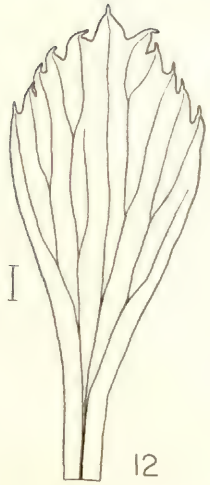


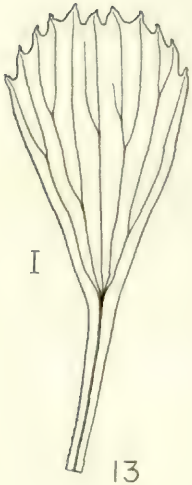
Foster, Venation in Circaeaster

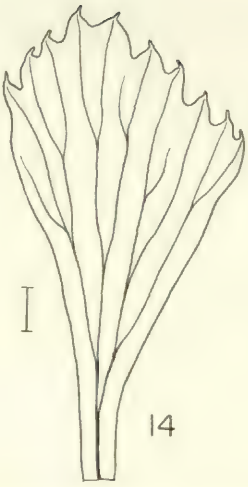
Foster, Venation in Circaeaster

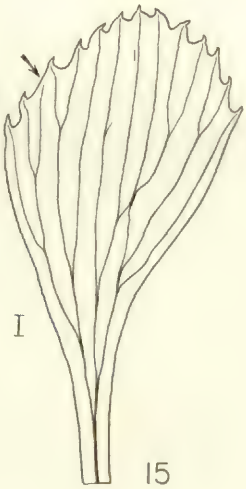




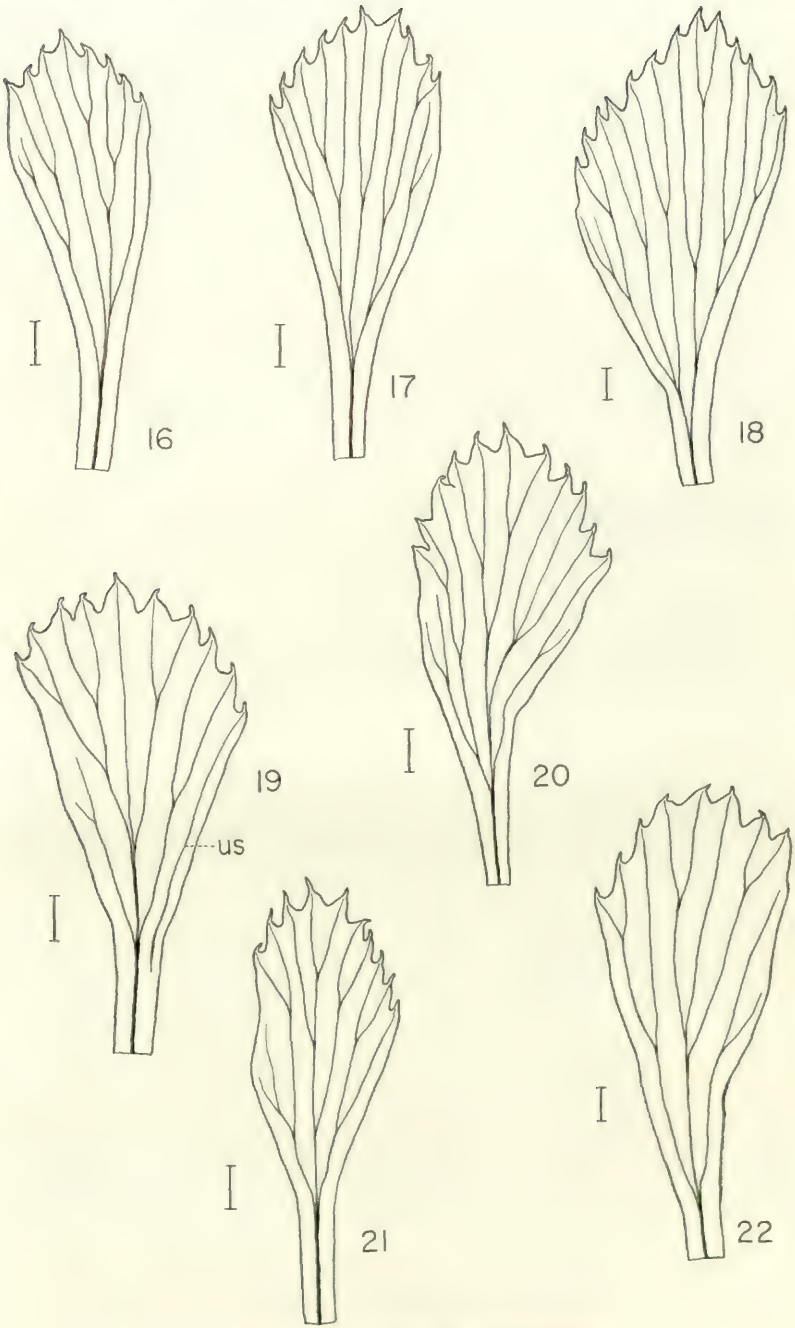








FOSTER, VENATION IN CIRCAEASTER



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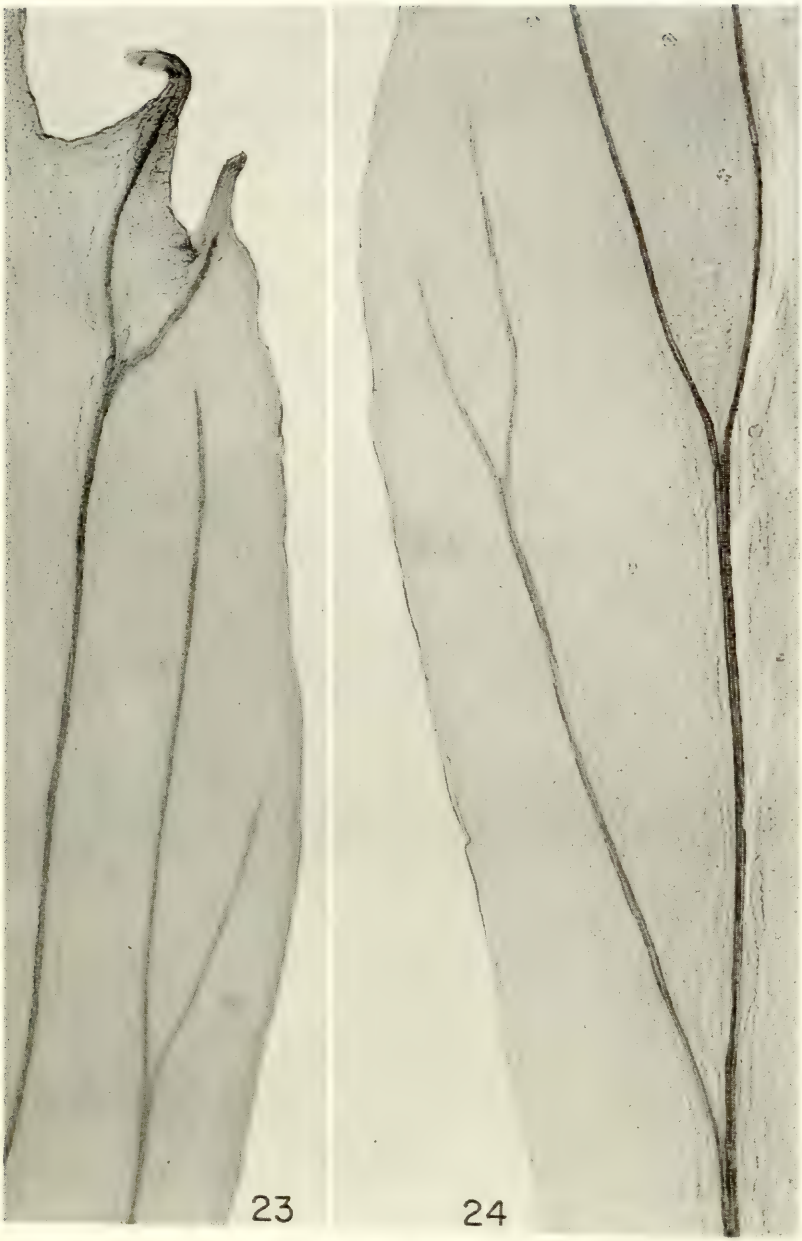
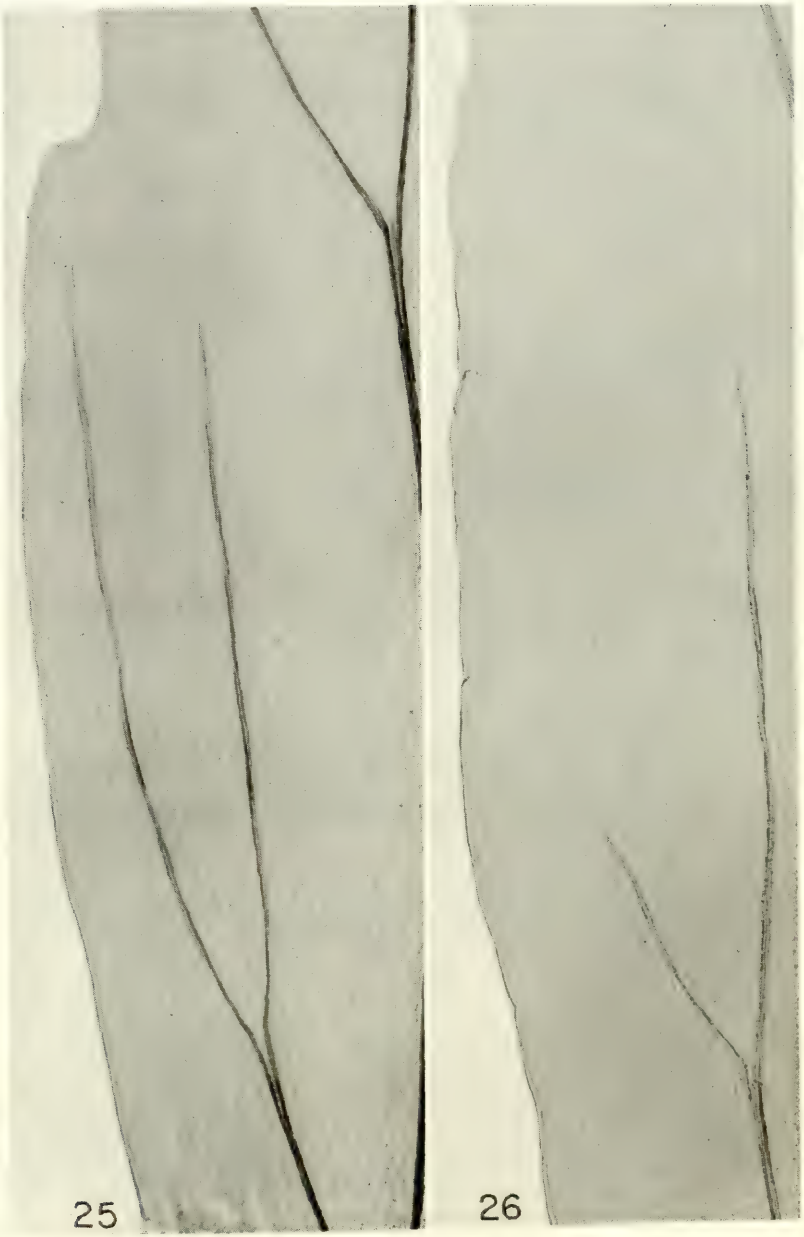


Foster, Venation in Circaeaster



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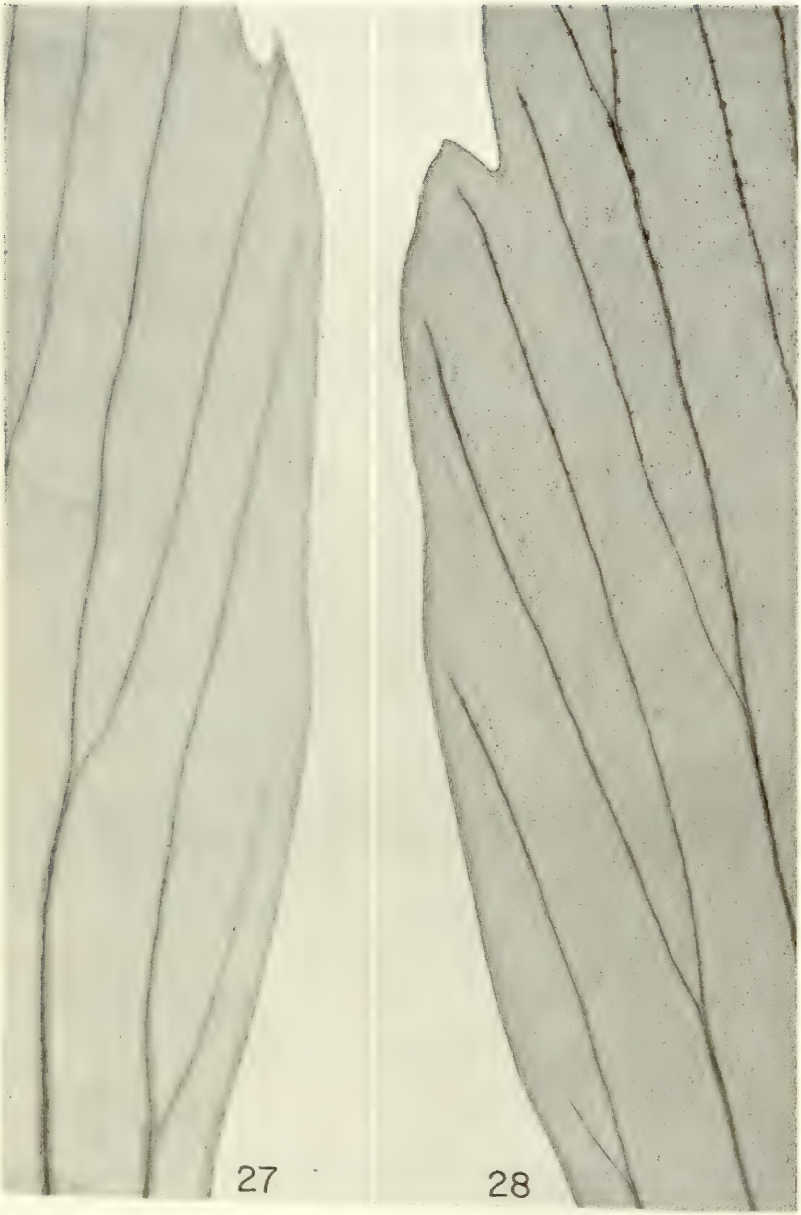

FOSTER, VENATION IN CIRCAEASTER

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, V. LEAF ANATOMY*

WILLIAM C. DICKISON

IN THE PRECEDING PAPER in this series (Dickison, 1969) I discussed the significance of nodal and leaf vascularization. The present article represents an extension of that study surveying additional features of leaf anatomy. It is hoped that the new information presented will help clarify the taxonomy, evolution, and generic definitions in this tropical family. All specimens studied have been cited with their respective collection data in my last paper. Though the lack of a complete collection of liquid-preserved specimens often prevented comparative observations, several new anatomical features are reported for the first time in the family.

Continued examination of leaf vascularization in the family has revealed a truly impressive range of variation, particularly in *Hibbertia*. In addition to differences in vein diameter and presence or absence of sheathing sclerenchyma pointed out earlier, the pattern and orientation of the veins is often diagnostic. For example, *H. glaberrima* can be distinguished by the orientation of veins at right angles to the long axis of the leaf (FIGURE 46), whereas *H. tomentosa* is characterized by a closed venation pattern, i.e., very few free vein endings. A careful investigation of this variation using a wide range of material might prove to be of unusual taxonomic importance. I have already drawn attention to the characteristic leaf venation of many needle-leaved hibbertias, viz., a prominent midvein with recurved laterals. The massive nature, in some species, of recurved secondary veins, as they terminate at the leaf base is illustrated by FIGURES 31 and 33. The extensive development of tracheary elements in this region of the leaf is not only of anatomical interest, but raises questions about possible physiological factors involved.

FOLIAR IDIOBLASTS

Foster (1956), in his review of plant idioblasts, recognizes three major categories of idioblastic cells — excretory, tracheoid, and sclerenchymatous. Examples of each class are found in leaves of the Dilleniaceae.

Excretory idioblasts. A common component of this heterogeneous assemblage are crystalliferous idioblasts. The occurrence of enlarged, raphide-containing cells is frequently cited as a primary character distinguishing the Dilleniaceae from other putatively related families (e.g., Cronquist, 1968). Since the distribution of raphides is limited in dicotyle-

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dons, their presence assumes greater taxonomic importance than other more common crystal types (Metcalfe & Chalk, 1950). Gibbs (1958) is of the opinion that the presence of raphides is a primitive feature.

Raphides have been observed in the leaves of all dilleniaceous genera except *Schumacheria*. Crystals were found with equal frequency in both the petiole and lamina; however, within the lamina, there is a tendency for raphides to be restricted to either the spongy or palisade mesophyll. Those found in the palisade layers are usually orientated in an upright manner (FIGURE 27). The needle-like raphides are often produced in enlarged, thin-walled idioblasts containing an abundance of mucilage (FIGURES 5, 21, 27). Calcium oxalate is deposited early in ontogeny as shown by the occurrence of crystals in the hypocotyl and cotyledons of *Dillenia*, *Hibbertia*, and *Tetracera* (FIGURE 20).

Crystals intermediate in shape between raphides and crystal sand are prevalent in some members of the family, e.g., *Curatella*. Examples of this condition may be seen in the enlarged pith parenchyma cells of the midrib in *Doliocarpus olivaceus* (FIGURE 22). The "crystal complement" of the family also includes cuboidal and nearly prismatic crystals as observed in the petiole of *Doliocarpus guianensis* (FIGURE 56) and *Hibbertia pancheri*. The latter types have not previously been reported.

The distribution of crystalliferous cells in the phloem parenchyma of the petiole and midrib was noted by Metcalfe and Chalk (1950) in *Hibbertia scandens* (FIGURE 23). This condition seems to be characteristic of the family as a whole, having now been observed in *Curatella*, *Didesmandra*, *Dillenia*, *Doliocarpus*, and *Tetracera*.

The presence of silica containing cells in the Dilleniaceae has been known for some time. Workers have noted silicified cells in *Curatella*, *Davilla*, *Doliocarpus*, *Hibbertia*, and *Tetracera*. Silica deposition occurs throughout the parenchymatous regions of the leaf mesophyll and epidermis as either fine granular particles within the cell lumen (FIGURE 54), or larger bodies impregnating the cell wall and intercellular cavities (FIGURE 55). The abundance of these silica deposits, combined with crystals and sclerified trichomes, makes it possible to use the leaves of *Curatella*, *Davilla*, and *Tetracera* as sandpaper (Standley & Williams, 1961).

Representing a third type of excretory idioblast of Dilleniaceae are the widely distributed "mucilaginous cells" (FIGURE 57). It is of particular interest that Parmentier (1896) referred to the presence of "cellules oléigènes" in the mesophyll of *Hibbertia scabra* and suggested their occurrence was an excellent character to show the affinities of the Dilleniaceae to the Magnoliaceae. Although the chemical nature of the cell mucilage is unknown, these idioblasts do not appear comparable to the "ethereal oil cells" of many ranalian families. The large oil sac or drop, as well as scent, described by Wilson (1965) as being characteristic of ranalian oil cells is lacking. Structurally, the enlarged mucilage cells differ considerably in size and form. Intergradations with raphide-containing idioblasts are common.

Tracheoid idioblasts. Cleared leaves of *Hibbertia montana* (*E. H.*

Wilson 476), *H. vestita* (NSW *55998*), and *H. subvaginata* (*C. L. Wilson 764*) revealed idioblasts which closely resemble the tracheoid type (FIGURE 47). The cells in question resemble typical tracheids in their spirally-thickened walls, general size and form, but are found completely isolated from other venation. They never occur in abundance. No evidence of undifferentiated procambium is present between these cells and the leaf vein. It is assumed, accordingly, that they arise in the lamina from the ground meristem. The best classification of these cells would probably be "storage tracheids" although there is no evidence to support their water-storing capacity.

The occurrence of elements of this sort in *Hibbertia* is of particular interest. Emphasis has already been put on the highly diverse vein endings in many species of this genus and a varied foliar sclereid composition will be described subsequently. It is evident, therefore, that within this single taxon is present a wide diversification of idioblast morphology. Foster (1956) pointed out that the morphological relationship between the various foliar idioblasts represents a complex problem which merits further careful study. I would suggest that *Hibbertia* represents extremely favorable material for such an investigation.

Sclerenchymatous idioblasts. Sclerenchymatous vein sheathing is present in the leaves of many Dilleniaceae (Dickison, 1969). This sclerenchyma, which often becomes massive (FIGURE 32), and encloses the terminal tracheids, is encountered in the petiole in the form of perivascular fibers (see Esau, 1965, p. 209) either capping vascular bundles or forming a continuous cylinder. In the larger veins of the lamina, sheathing extends from the adaxial to the abaxial surface.

The first report of sclereids in leaves of Dilleniaceae was by Steppuhn (1895) who described the occurrence of thick-walled, branched "spicular" cells in two species of *Hibbertia*. Further comprehensive examination, however, has revealed a much wider range of foliar sclereid morphology and distribution. Although sclereids are wide-spread in the family, they reach greatest diversity in *Hibbertia*. On the basis of their distribution, it is convenient to distinguish four types: (1) sclereids diffuse in the mesophyll (and pith and cortex of petiole), (2) sclereids terminal at vein endings, (3) epidermal sclereids, and (4) sclereids subtending trichomes.

With regard to the first category, various forms of sclereids are present: clusters of unbranched brachysclereids ("stone cells") are occasionally found in large numbers in the cortex and pith in petioles of *Davilla*, *Doliocarpus* (FIGURE 56), *Hibbertia* and *Schumacheria*; FIGURE 9 shows an abundance of these sclereids in the leaf base of *Hibbertia altigena*; in addition to the elongate sheathing fibers, the midvein of several species may also be enclosed by short, unbranched sclereids. In one collection of *Doliocarpus major* (*von Wedel 2860*) such sclereids are located along the periphery of the lamina (FIGURE 7). The conspicuous sclereids in *Hibbertia lucida* (FIGURE 3), *H. oubatchensis* (FIGURE 2), *H. pancheri*, and *H. patula* (FIGURE 1) all tend to be irregularly branched. These "armed," thick-walled sclereids occur in clusters throughout the mesophyll and

parenchymatous regions of the petiole. Very distinctive osteosclereids are present in the lamina of *H. salicifolia* (FIGURE 4). The latter cells, for the most part, are oriented with their long axis parallel to the long axis of the leaf. A fourth form of diffuse idioblast is the truly stellate sclereid (astrosclereids) found in the lamina of *H. crenata* (FIGURE 13).

In contrast to the above conditions, sclereids in *Hibbertia lasiopus*, *H. miniata*, *H. montana*, *H. obtusifolia*, and *H. saligna* are prevailingly associated with terminal veinlets. In the leaves of *H. lasiopus* (*C. L. Wilson 781*), *H. miniata* (*C. L. Wilson 782*), *H. montana* (*C. L. Wilson 838*), and *H. obtusifolia* (*Pullen 3882*) the idioblasts are parenchymatous, mostly unbranched, or provided with only rudimentary branches, and occur in clusters at, or in the vicinity of, the terminal tracheids (FIGURE 10). Along the margin of the lamina, however, are located extensively branched, stellate sclereids (FIGURE 11).

The terminal idioblasts of *Hibbertia saligna* (*Constable 43107*), on the other hand, are highly branched and occur singly at virtually all vein endings (FIGURE 12). In his paper on the terminal sclereids in *Mouriria*, Foster (1946) describes terminal cells intermediate in character between normal tracheary elements and sclereids. I have observed similar "transitional cells" in *Hibbertia*, again indicating the possible ontogenetic relationship between terminal sclereids and terminal tracheary elements. When the various terminal idioblastic cells described in my previous paper (Dickison, 1969) are considered in conjunction with the terminal sclereids now reported, the tremendous diversity of vein endings in this genus becomes evident.

Next to be considered is epidermal sclerification, which, once again, is present in *Hibbertia*. Of particular note are the massive, thick-walled cells in the upper epidermis of *H. nana*. The striking nature of these isolated sclereids may be seen in surface view in FIGURE 8. In sectioning, these cells are usually torn free leaving behind large spaces in the hypodermis (FIGURE 26). In many of the needle-leaved hibbertias, the entire epidermis becomes sclerified. Depending upon the species, the epidermal cells have wavy anticlinal walls (e.g., *H. mucronata*, FIGURE 6), or straight walls with overlapping ends (e.g., *H. acicularis*, FIGURE 48). Sclerification of the epidermis in these species appears to be a specialization related to the xerophytic habit. Another unique feature observed only in *Dillenia ochreata* was the intensive sclereid development in the petiole wings (FIGURE 5).

The last diagnostic sclereids in the leaves of Dilleniaceae are those which subtend the spiny, sclerified trichomes in *Tetracera*. This condition, which was first reported by Solereder (1908), has been observed only in the African species *T. leiocarpa*, the New World species *T. ovalifolia* and *T. portobellensis*, and an unnamed Krukoff collection from Brazil (*Krukoff 6430*). As seen in FIGURES 14, 15, and 17, these columnar cells traverse the mesophyll immediately under the compound trichomes. Usually only a single sclereid is present under each trichome fascicle, but in the Krukoff collection a large cluster of sclereids is present. Although these sclereids

are typically unbranched, they may become branched to varying degrees (FIGURE 16). The relationship between trichomes and sclereid formation in these plants is not clear. Their limited distribution, however, suggests they are of good systematic value. Moreover, the entire range of sclereid morphology in the family appears to be of potential taxonomic importance.

TRICHOMES

The scabrous nature of dilleniaceous leaves is well known to those familiar with the family. Solereder (1908) and Metcalfe and Chalk (1950) describe the trichome composition as consisting of simple unicellular, stellate, and rarely peltate hairs. The complete trichome complement of the family, however, has never been adequately illustrated.

Simple unicellular trichomes are the most common form in the family, being present in all genera. Significant fluctuations are found in the length, form, and distribution of these hairs. Gradations in length occur from the narrow, very elongate (up to 1600μ) trichomes in species of *Acrotrema* (FIGURE 41), *Didesmandra* and *Dillenia*, to the very short, pointed type seen in *Doliocarpus* (FIGURE 44). These hairs may be thick-walled, straight and highly sclerified (FIGURES 13, 26), or, thin-walled and curled (FIGURES 19, 59). Distinctive short, thick-walled, curved hairs are present on the lower epidermis of *Hibbertia baudouinii* (FIGURE 28). Simple unicellular trichomes also may become silicified (e.g., *Davilla*).

Stellate trichomes are present in *Curatella* (FIGURE 45) and *Hibbertia* (FIGURES 30, 34). Various forms of fasciculate trichomes with unicellular rays are common in the family. In *Curatella* (FIGURE 45), *Didesmandra* (FIGURE 43), and *Tetracera* (FIGURES 14, 15) the rays are reduced to spines. Gradation between spiny fascicles and the stellate condition can be seen in FIGURES 17 and 58. The walls of these cells are sclerified and/or incrusted with silica. Although peltate hairs have been reported for *Hibbertia lepidota*, I have not observed true peltate trichomes during this study. I do not believe, furthermore, that the drawing by Solereder (*loc. cit.*, p. 22) represents a truly peltate condition but rather an asteroid modification of the fasciculate type.

A short, highly silicified, blunt-tipped, papillate trichome is prevalent in many species of *Dillenia* (FIGURES 40, 60, 61). In surface view these trichomes are irregular in outline (FIGURE 61). In some species this may be the only type of trichome present. In species which possess both unicellular and papillate trichomes, their distribution seems to be of diagnostic value (see FIGURES 60, 61).

Although the Dilleniaceae have long been thought to lack glandular trichomes, I am now reporting this feature for the first time in the family. Trichomes with typical glandular morphology, i.e., stalk and multicellular head, were found in *Dillenia philippinensis* and *D. reifferscheidia*. FIGURE 39 shows their location in depressions on the abaxial surface of the lamina.

EPIDERMIS AND STOMATA

Following the early work of Parmentier (1896), the Dilleniaceae have been regarded by subsequent investigators (e.g., Solereder, 1908, and Metcalfe & Chalk, 1950) as possessing stomata of the ranunculaceous (anomocytic) and rubiaceous (paracytic) types. A lack of adequate liquid-preserved specimens has prevented critical observations on the epidermis of *Acrotrema*, *Doliocarpus*, and *Schumacheria*; nevertheless, my preliminary studies reveal a wider range of structural variation than previously suspected. Although the systematic significance of this variation cannot be assessed at present, the type of stomatal apparatus, size of guard cells, size and undulation of ordinary epidermal cells, and presence of cuticular striations appear to be of potential taxonomic value.

Stomata are confined without exception to the abaxial leaf surface (FIGURE 27). In many hibbertias they are located in stomatal crypts or grooves. Stomatal crypts are prevalent among many New Caledonian species, e.g., *H. baudouinii* (FIGURE 28), *H. nana* (FIGURE 26), *H. pancheri* (FIGURE 25), *H. pulchella*, *H. tontoutensia*, *H. trachyphylla*, and *H. wagapii*. Stomatal grooves extending the length of the lamina are characteristic of most xerophytic, needle-leaved Australian species. Differences occur in the shape of the groove and in the trichome distribution. *Hibbertia pungens* (FIGURE 35) illustrates a condition where hairs completely fill the groove. In *H. uncinata* (FIGURE 37) trichomes are located only at the opening whereas in *H. pachyrhiza* (FIGURE 36) the grooves lack trichomes. FIGURE 36 also shows the thick cuticle formation in many of these species along with prominent striations.

The leaves of *H. gilgiana* are distinguished by the anticlinal walls of both upper and lower epidermal cells being arched at the point of contact (FIGURE 29). It can also be seen that the stomata are noticeably raised. A conspicuously papillate epidermis is also present in many species (e.g., *H. baudouinii*, FIGURE 28).

Reference has previously been made to elongate, sclerified epidermal cells in xerophytic hibbertias (FIGURE 48). The outer wall of these cells is frequently thickened and provided with papillae. Epidermal cells surrounding the spiny, fasciculate trichomes become differentiated by their thickened walls and lack of undulation. The epidermal cells of *Doliocarpus olivaceus* appear very distinctive in being circular and highly undulate. Unfortunately I did not have good material for study of this species. Silicification of the epidermis has been noted in *Curatella* (FIGURE 45), *Davilla*, *Didesmandra*, *Dillenia*, *Hibbertia*, and *Tetracera*.

With regard to stomatal apparatus, *Tetracera* and *Didesmandra* possess the rubiaceous type. The two parallel subsidiary cells are distinguishable from the surrounding epidermal cells by their shape and dark contents (FIGURE 50). Guard cells vary in length from 20 to 35μ. The epidermis of *Didesmandra* is perhaps the most distinctive in the family. The anticlinal walls of epidermal cells are undulate, guard cells lack chloroplasts, and

cuticular striations are orientated at right angles to the obliquely orientated subsidiary cells (FIGURE 49).

The stomatal structure in *Curatella*, *Davilla*, *Dillenia*, and *Hibbertia* is predominantly ranunculaceous, since no subsidiary cells are evident (FIGURE 53). Considerable variation does occur, however, in the undulation of epidermal cells and size of guard cells. Within the family guard cells range in length from 16 to 36μ. Uniformly small guard cells (under 20μ) were found in *Curatella*, *Davilla*, *Dillenia ovata*, and *Doliocarpus major*.

Of particular interest is the stomatal apparatus encountered in *Hibbertia tetrandra*. A careful examination showed it to be unlike all other Dilleniaceae examined, as it could properly be classified as "gordoniaceous" (FIGURE 51). The gordoniaceous stomatal apparatus (*sensu* Keng, 1962) is described as consisting of guard cells surrounded by two to four subsidiary cells which differ from ordinary epidermal cells in narrower cell shape and in their reaction to chemical reagents. In *Hibbertia* the number of subsidiary cells varies from four to six. Keng (*loc. cit.*) tentatively named this stomatal apparatus for the theaceous genus *Gordonia* in which it was first described by Solereder (1908), who has subsequently considered it as characterizing the subfamily Camellioideae of the Theaceae.

In view of the apparent restricted distribution of the gordoniaceous type of stomatal apparatus, its presence in the Dilleniaceae seems to be of special significance in relating these two families.

MESOPHYLL

The mesophyll of dilleniaceous leaves displays considerable differentiation at both generic and specific levels. Each genus has a distinctive combination of characters. In addition to the specialized idioblasts already mentioned, anatomical features of the mesophyll which demonstrate variation are: thickness, presence or absence of a hypodermis and its location on the adaxial or abaxial surface, bifacial or isolateral nature, number of palisade layers, and presence or absence of intercellular spaces in the spongy layers. A comparison of these features in all genera excluding *Hibbertia* is listed in TABLE 1. It should be noted that a hypodermis is found in some species of *Dillenia*. Also, the correlation between the coriaceous texture of the leaf, its multiple palisade layers, and a complex petiolar anatomy is noteworthy in *Doliocarpus*.

The largest number of anatomical specializations, however, is found in the leaves of *Hibbertia* where extreme adaptations to environment have occurred. A few selected species listed in TABLE 2 exemplify the range of diversification.

DISCUSSION

In response to extremes in the habitat, the leaves of Dilleniaceae exhibit marked differences in form, texture and thickness. Correlated with external

TABLE 1. **Anatomical Comparison of Leaf Mesophyll in Dilleniaceae** (excluding *Hibbertia*).

TAXON	NUMBER OF LAYERS IN ADAXIAL HYPODERMIS	NUMBER OF LAYERS IN ABAXIAL HYPODERMIS	NUMBER OF PALISADE LAYERS	INTERCELLULAR SPACES
Acrotrema (adequate material not available for study)				
Curatella (FIG. 45)	—	—	2, ± isolateral	sparse
Davilla	—	—	2	sparse
Didesmandra (FIG. 43)	—	—	1	abundant
Dillenia excelsa	1	—	2–3	moderate
D. indica	—	—	2	moderate
D. megalantha	1–2	—	2	moderate
D. ovata	—	—	1	moderate
D. papuana	2	—	2–3	abundant
D. philippinensis	1	—	1	moderate
D. pulchella (FIG. 38)	2	1	2	moderate
D. reifferscheidia (FIG. 39)	1–2	1–2	2	moderate
D. suffruticosa (FIG. 40)	—	—	2–3	abundant
Doliocarpus sp. (*Pires et al. 52254*)	—	—	3	sparse
D. calineoides (FIG. 44)	—	—	2	moderate
D. coriaceus	—	—	2–3	sparse
D. dentatus	—	—	1	moderate
D. guianensis	—	—	2–3, ± isolateral	moderate
D. lasiogyne	—	—	1–2	sparse
D. olivaceus (FIG. 42)	—	—	1	abundant
Schumacheria castaneifolia	—	—	2–3	abundant
Tetracera indica	—	—	1	moderate
T. scandens (FIG. 18)	—	—	2–3	moderate

differences, are a number of highly divergent trends of anatomical specialization which parallel those that occur in the dicotyledons as a whole.

In arid environments, dilleniaceous leaves have become either increasingly coriaceous or reduced in size. Coriaceous leaves are generally distinguished by formation of multiple palisade layers, a tendency to become isolateral, an absence of intercellular spaces, sclerification of trichomes, intensive sclerification along the veins and veinlets, formation of sclereid clusters in the mesophyll, and in *Hibbertia*, development of abaxial stomatal crypts. In *H. patula* a tremendous increase in leaf thickness is the result of extensive development of spongy mesophyll.

In other hibbertias, in contrast, (e.g., *H. gilgiana*) the lamina has become reduced in thickness resulting in a poorly differentiated mesophyll.

Progressive reduction in leaf size in *Hibbertia* has proceeded along several distinct lines. The result of this specialization is the production of reduced leaves of very diverse form and shape. The ultimate reduction in leaf evolution has taken place in the genus *Pachynema* where only scale-like projections are present (although they are still morphologically megaphylls). Xerophytic modification is evident in the ericoid habit, the

TABLE 2. Anatomical Comparison of Leaf Mesophyll in Hibbertia

TAXON	HYPODERMIS (MULTIPLE EPIDERMIS?)	NUMBER OF LAYERS IN PALISADE	ABAXIAL PALISADE	ABAXIAL CRYPTS OR GROOVES	INTERCELLULAR SPACES	LEAF FORM AND TEXTURE
H. cuneiformis (FIG. 27)	—	1	—	—	moderate	flat
H. baudouinii (FIG. 28)	—	2	—	crypts	sparse	flat
H. gilgiana (FIG. 29)	mesophyll not clearly differentiated			—	moderate	flat-thin
H. nana (FIG. 26)	1 layered	1	+	crypts	sparse	flat-coriaceous
H. pancheri (FIG. 25)	—	2–3 (4)	—	crypts	moderate	flat
H. patula (FIG. 24)	—	1–2 (extensive spongy mesophyll	—	sunken stoma	abundant	flat-thick
H. pungens (FIG. 35)	—	1	+	grooves	moderate	ericoid
H. sericea (FIG. 30)	—	1	—	—	moderate	inrolled margins
H. teretifolia	—	1	+	—	sparse	terete

lamina with inrolled margins, and in *H. teretifolia*, a terete leaf form. Such specializations are often associated with intensification of vascularization and reflexed venation, sclerification of trichomes and epidermal cells, formation of abaxial palisade, and absence of intercellular spaces. It is interesting to note that the needle-leaved hibbertias generally do not exhibit sclerified vein sheathing.

In both the broad-leaved and needle-leaved species of *Hibbertia*, there has also occurred a wide range of morphological diversification of the terminal tracheary elements. It is evident, accordingly, that the anatomy of the dilleniaceous leaf, in many instances, has become highly specialized and directly reflects the modifying influence of environmental extremes.

Carlquist (1961) indicated that the leaf is perhaps anatomically the most varied organ of angiosperms, and as a result often contains numerous characters of taxonomic importance. Leaf anatomy of the Dilleniaceae has been shown to possess a considerable amount of variation which heretofore has not been fully exploited for systematic purposes. When the nodal and petiolar anatomy is considered in conjunction with characters from the lamina, the dilleniaceous genera are sharply defined. In many instances, excellent specific characters have been pointed out as well.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Foliar sclereids. FIG. 1, *Hibbertia patula* (*McKee 3543*), sclereids photographed in polarized light between crossed nicols, × 51. FIG. 2, *H. oubatchensis* (*McKee 3306A*), × 132. FIG. 3, *H. lucida* (*C. T. White 2210*), × 208. FIG. 4, *H. salicifolia* (*C. L. Wilson 625*), cleared leaf showing elongate osteosclereids oriented parallel to long axis of leaf, × 51.

PLATE II

FIGS. 5–9. Foliar sclereids. FIG. 5, *Dillenia ochreata* (NIFS *bb18085*), cleared petiole wing showing extensive sclereid development, × 52. FIG. 6, *Hibbertia mucronata* (*C. L. Wilson 792*), cleared leaf showing epidermal sclereids with undulating anticlinal walls, × 52. FIG. 7, *Doliocarpus major* (*von Wedel 2860*), cleared leaf showing unbranched sclereids along margin of lamina, × 132. FIG. 8, *Hibbertia nana* (*Baumann-Bodenheim 15358*), cleared leaf showing massive epidermal sclereids, × 52. FIG. 9, *H. altigena* (*McKee 3709*), base of leaf containing numerous unbranched sclereids, × 52.

PLATE III

FIGS. 10–13. Foliar sclereids. FIG. 10, *Hibbertia lasiopus* (*C. L. Wilson 781*), note sclereids tend to be situated at vein endings, × 52. FIG. 11, *H. montana* (*C. L. Wilson 838*), cleared leaf photographed in polarized light between crossed nicols. Note extensively branched sclereids along periphery of lamina, × 52. FIG. 12, *H. saligna* (*Constable 43107*), cleared leaf showing branched, terminal sclereids, × 133. FIG. 13, *H. crenata* (*C. L. Wilson 851*), transverse section of lamina showing stellate sclereids in mesophyll and sharply pointed, sclerified trichomes, × 209.

PLATE IV

FIGS. 14–19. Leaf anatomy of *Tetracera*. FIG. 14, *T. ovalifolia* (*Johnston 1140*), cleared leaf showing compound, sclerified trichomes with subtending sclereids (arrows), × 52. FIG. 15, *the same*, transverse section of lamina, × 208. FIG. 16, *T. leiocarpa* (*Cooper 45*), isolated branched sclereid illustrating thick, pitted wall, × 520. FIG. 17, *T. portobellensis* (*Steinbach 7229*), transverse section of lamina showing sclerified, fasciculate trichomes with subtending sclereids, × 208. FIG. 18, *T. scandens* (*M. Q. Lagrimas s.n.*, Makiling, Philippines), transverse section of leaf, × 208. FIG. 19, *T. boiviniana* (*Tanner 2548*), transverse section of lamina showing undulating abaxial surface and curled trichomes, × 208.

PLATE V

FIGS. 20–23. Varied forms of crystals in leaves. FIG. 20, *Tetracera indica* (seedling grown from seed supplied by H. Keng), cleared cotyledon showing numerous raphides, × 54. FIG. 21, *T. akara* (*Elmer 21314*), cleared leaf showing raphide-containing idioblast. Also note the much branched mesophyll parenchyma, × 210. FIG. 22, *Doliocarpus olivaceus* (*Stern et al. 11*), transverse section of midrib showing enlarged, crystal containing pith cells. The crystals are transitional between raphides and crystal sand. Also note the complete vascular cylinder and the lack of medullary bundles, × 135. FIG. 23, *Hibbertia scandens* (*Cult.* E *C4386*), transverse section of midrib illustrating enlarged crystal-containing phloem parenchyma cells, × 210.

PLATE VI

FIGS. 24–30. Leaf anatomy of *Hibbertia*. FIG. 24, *H. patula* (*McKee 3543*), transverse section showing extensive mesophyll development, sunken stomata (st), foliar sclereids, and sclerenchyma surrounding vein, × 54. FIG. 25, *H. pancheri* (*Thorne 28585*), transverse section showing multilayered palisade mesophyll and stomatal crypts, × 54. FIG. 26, *H. nana* (*Baumann-Bodenheim 15358*), transverse section showing hypodermis with epidermal sclereid torn free, isolateral mesophyll, stomatal crypt, and sclerified trichomes on lower surface, × 54. FIG. 27, *H. cuneiformis* (*Cult.* K *s.n.*), transverse section illustrating single layered palisade with raphide idioblast and stomata (st) on lower surface, × 132. FIG. 28, *H. baudouinii* (*Baumann-Bodenheim 11203*), transverse section showing lack of intercellular spaces in mesophyll, papillate lower epidermis, and short, curved trichomes (tr), × 52. FIG. 29, *H. gilgiana* (*C. L. Wilson 856*), transverse section of lamina illustrating weakly differentiated mesophyll, arching epidermal cells and raised guard cells (st), × 135. FIG. 30, *H. sericea* (*Muir 855*), transverse section showing stellate, sclerified trichomes, × 52.

PLATE VII

FIGS. 31–37. Leaf anatomy of *Hibbertia* [continued]. FIG. 31, *H. uncinata* (*E. H. Wilson 155*), basal portion of cleared leaf showing massive formation of tracheary elements in the recurved secondary veins, × 52. FIG. 32, *H. australis* (*Aston 359*), transverse section of midrib showing well-developed fibers on abaxial side, × 140. FIG. 33, *H. cistifolia* (*Specht 843*), transverse section of base of leaf illustrating prominent central midrib and extensive tracheary tissue on either side. Note absence of sheathing sclerenchyma, × 53. FIG. 34, *H. tomentosa* (*Specht 638*), surface view of stellate trichomes, × 135. FIG. 35, *H. pungens* (*Royce 7640*), transverse section of leaf showing ericoid habit. In this species trichomes completely fill the stomatal grooves. Also note adaxial and abaxial palisade layer, × 53. FIG. 36, *H. pachyrhiza* (*C. L. Wilson 861*), transverse section of stomatal groove showing absence of trichomes and wavy cuticle, × 210. FIG. 37, *H. uncinata* (*E. H. Wilson 155*), transverse section of stomatal groove showing trichome formation only at entrance, × 210.

PLATE VIII

FIGS. 38–45. FIG. 38, *Dillenia pulchella* (*Cult.* SING *s.n.*), transverse section of lamina showing adaxial and abaxial hypodermis. Large spaces represent sites of crystal deposition, × 132. FIG. 39, *D. reifferscheidia* (*M. Q. Lagrimas s.n.*, Quezon, Philippines), transverse section of lamina illustrating sunken, glandular trichome on lower surface, × 132. FIG. 40, *D. suffruticosa* (*Cult.* SING *s.n.*), transverse section of lamina showing silicified, papillate trichome (arrow) on lower surface, × 132. FIG. 41, *Acrotrema* sp. (US *1576875*), cleared leaf showing elongate, unbranched trichomes distributed along the major veins, × 22. FIG. 42, *Doliocarpus olivaceus* (*Stern et al. 11*), transverse section of lamina, × 135. FIG. 43, *Didesmandra aspera* (from Sarawak, *s.n.*), transverse section showing thin mesophyll and sclerified trichome, × 135. FIG. 44, *Doliocarpus calineoides* (*G. T. Prance et al. 3830*), transverse section showing two-layered palisade and short, spiny trichomes (tr) on lower surface. Separation of tissue is the result of preparation, × 135. FIG. 45, *Curatella americana* (*Irwin 5470*), transverse section of lamina illustrating lack of intercellular spaces, undulating abaxial surface, tendency toward isolateral mesophyll, silicification of epidermis, stellate and spiny trichomes, × 135.

PLATE IX

FIGS. 46–48. FIG. 46, *Hibbertia glaberrima* (*Perry 5379*), cleared leaf showing tendency of veins to be orientated at right angles to long axis of lamina, × 26. FIG. 47, *H. subvaginata* (*C. L. Wilson 764*), cleared leaf showing isolated tracheary idioblast, × 160. FIG. 48, *H. acicularis* (*Clemens 43622*), cleared leaf showing elongate epidermal sclerenchyma, × 160.

PLATE X

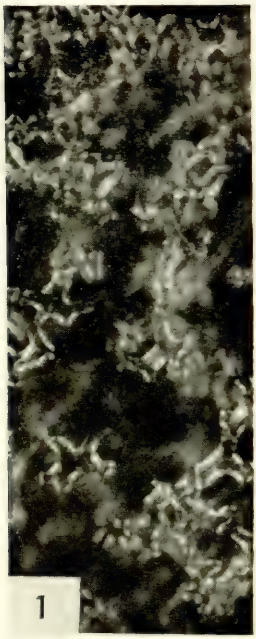
FIGS. 49–53. Lower epidermal layers of leaves preserved in FAA and mounted unstained. FIG. 49, *Didesmandra aspera* (from Sarawak, *s.n.*), note undulating anticlinal walls of epidermal cells, cuticular striations, and absence of chloroplasts in guard cells, × 163. FIG. 50, *Tetracera indica* (*H. Keng, s.n.*, from Singapore), note two parallel subsidiary cells (sc), × 163. FIG. 51, *Hibbertia tetrandra* (*Cult.* E *C3544*), "gordoniaceous" stomatal apparatus with five subsidiary cells (sc), × 650. FIG. 52, *H. dentata* (*Cult.* K *s.n.*), note undulating anticlinal walls of epidermal cells, prismatic bodies (arrow), and striations around stomatal apparatus, × 163. FIG. 53, *H. scandens* (*Cult.* K *s.n.*), note the epidermal cells are not wavy although they do possess primary pit fields. The stomatal apparatus is ranunculaceous, × 163.

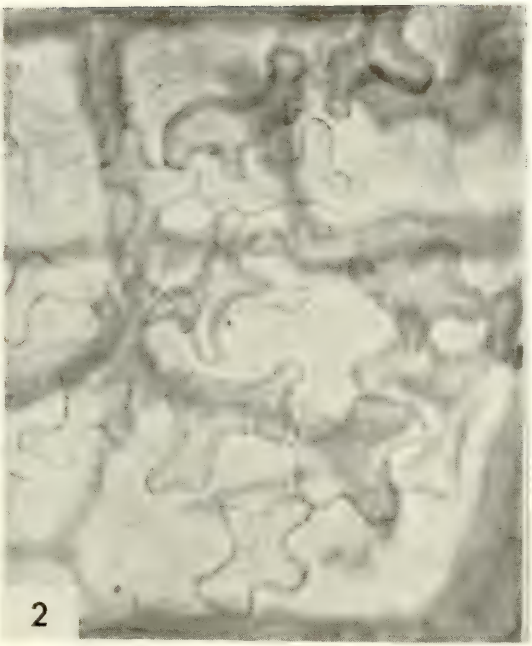
PLATE XI

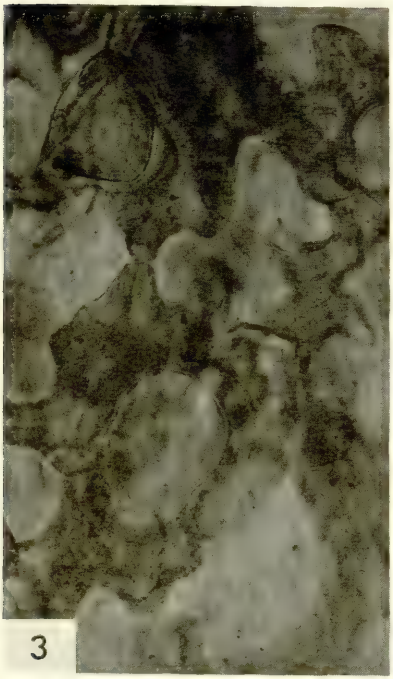
FIGS. 54–57. Foliar idioblastic cells. All. × 260. FIG. 54, *Davilla* sp. (*Irwin 5570*), transverse section of midrib showing silica-containing cells (arrow). FIG. 55, *Curatella americana* (*Irwin 5470*), transverse section of midrib showing silica deposits (arrows) and raphide idioblast in upper right. FIG. 56, *Doliocarpus guianensis* (UC *947180*), transverse section of petiole showing sclerotic cells and cuboidal crystals in cortex. FIG. 57, *Dillenia pulchella* (*Cult.* SING *s.n.*), arrow indicates enlarged, mucilaginous idioblast in cortical region of midrib.

PLATE XII

FIGS. 58–61. Foliar trichomes. FIG. 58, *Hibbertia stirlingii* (*C. L. Wilson 757*), transverse section of lamina illustrating sclerified, fasciculate trichome, × 240. FIG. 59, *H. coriacea* (*Humbert 5866*), transverse section of lamina showing abundance of curled, unicellular trichomes on lower surface, × 160. FIG. 60, *Dillenia cyclopensis* (*Van Royen* & *Sleumer 5812*), cleared leaf showing papillate trichomes restricted to veins, × 65. FIG. 61, *D. philippinensis* (*M. Q. Lagrimas s.n.*, Makiling, Philippines), cleared leaf showing irregular outline of papillate hairs and their general distribution over surface of lamina, × 160.







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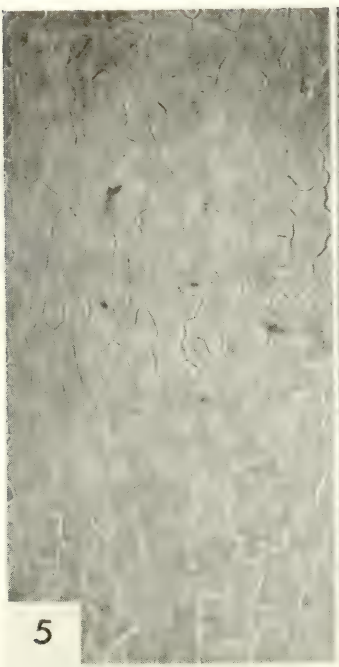

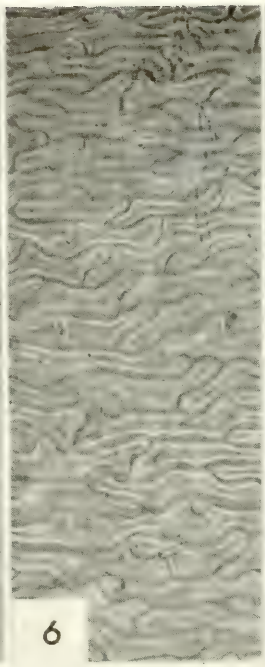

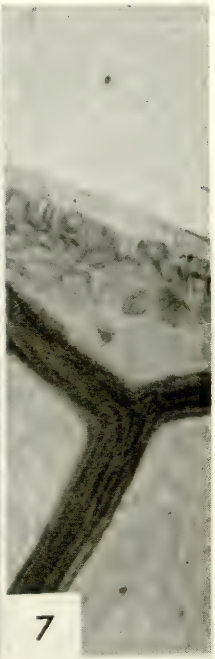

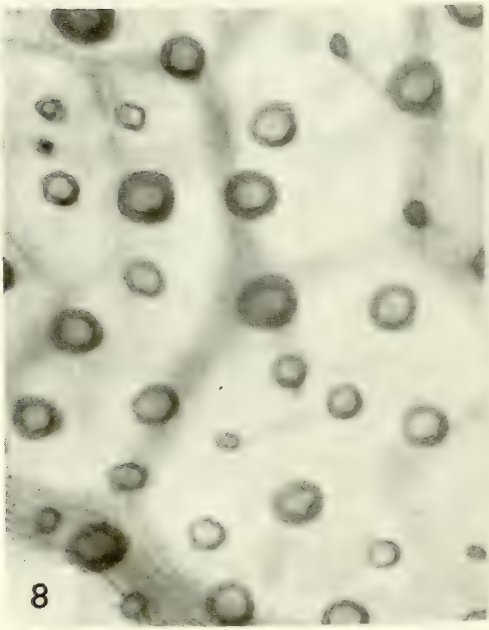

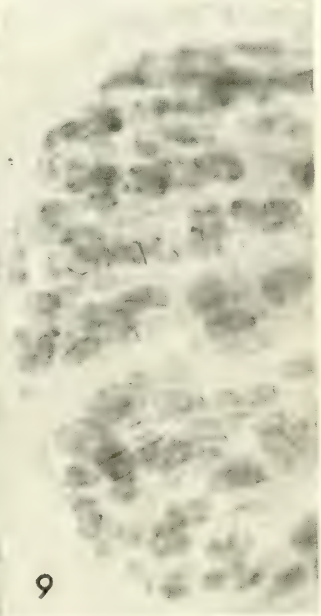

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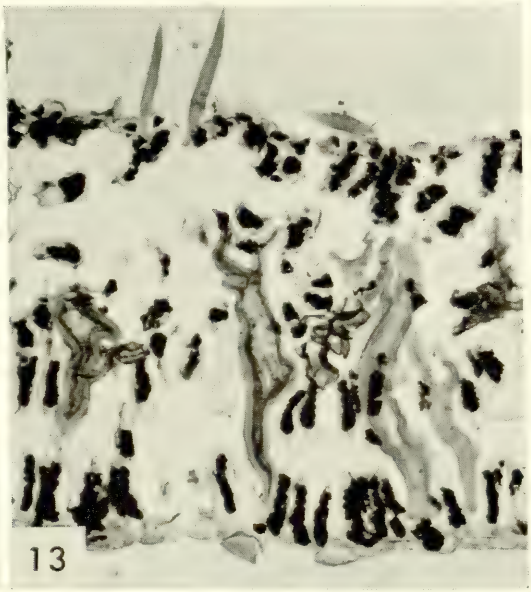
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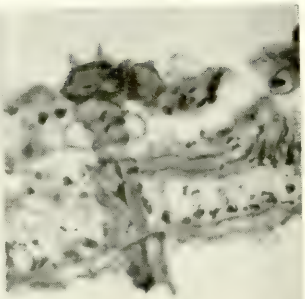
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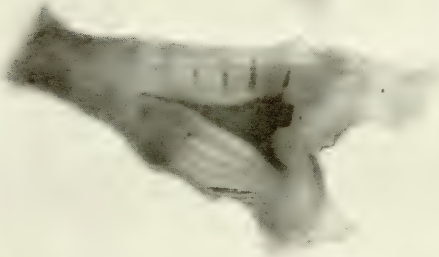
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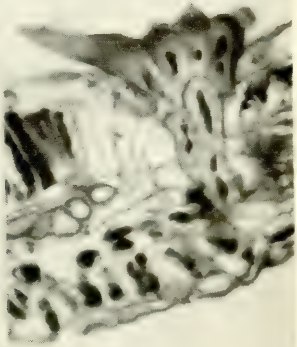
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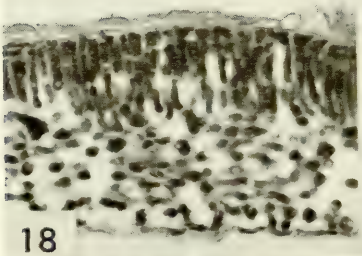
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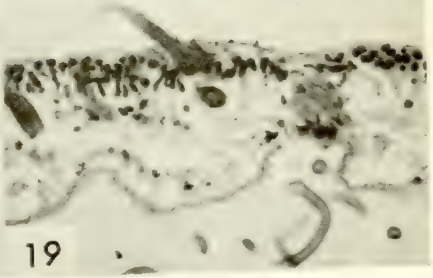
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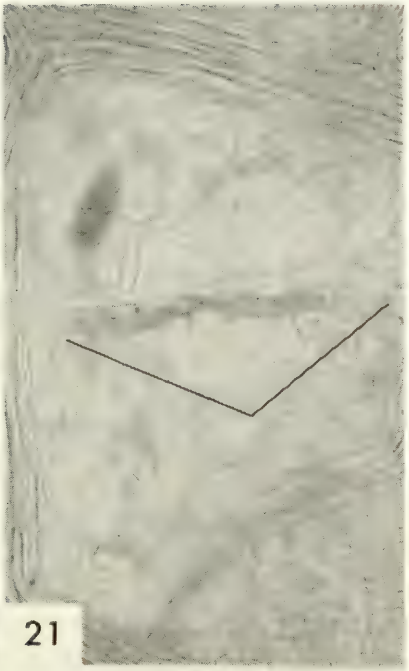
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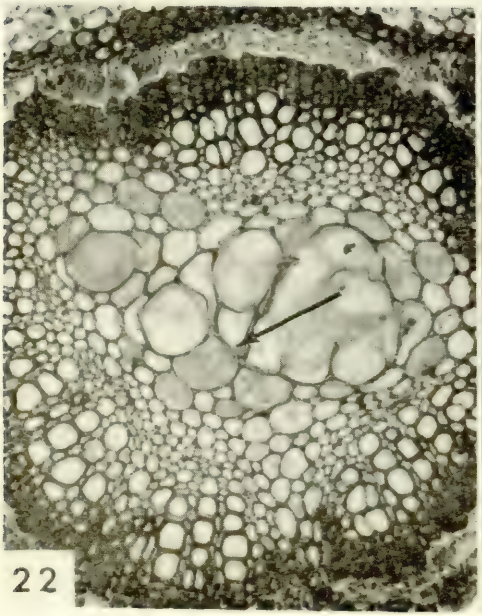
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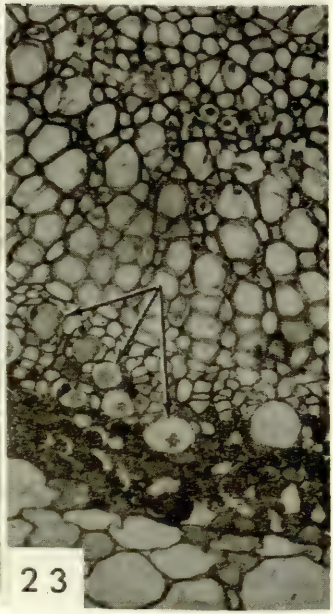
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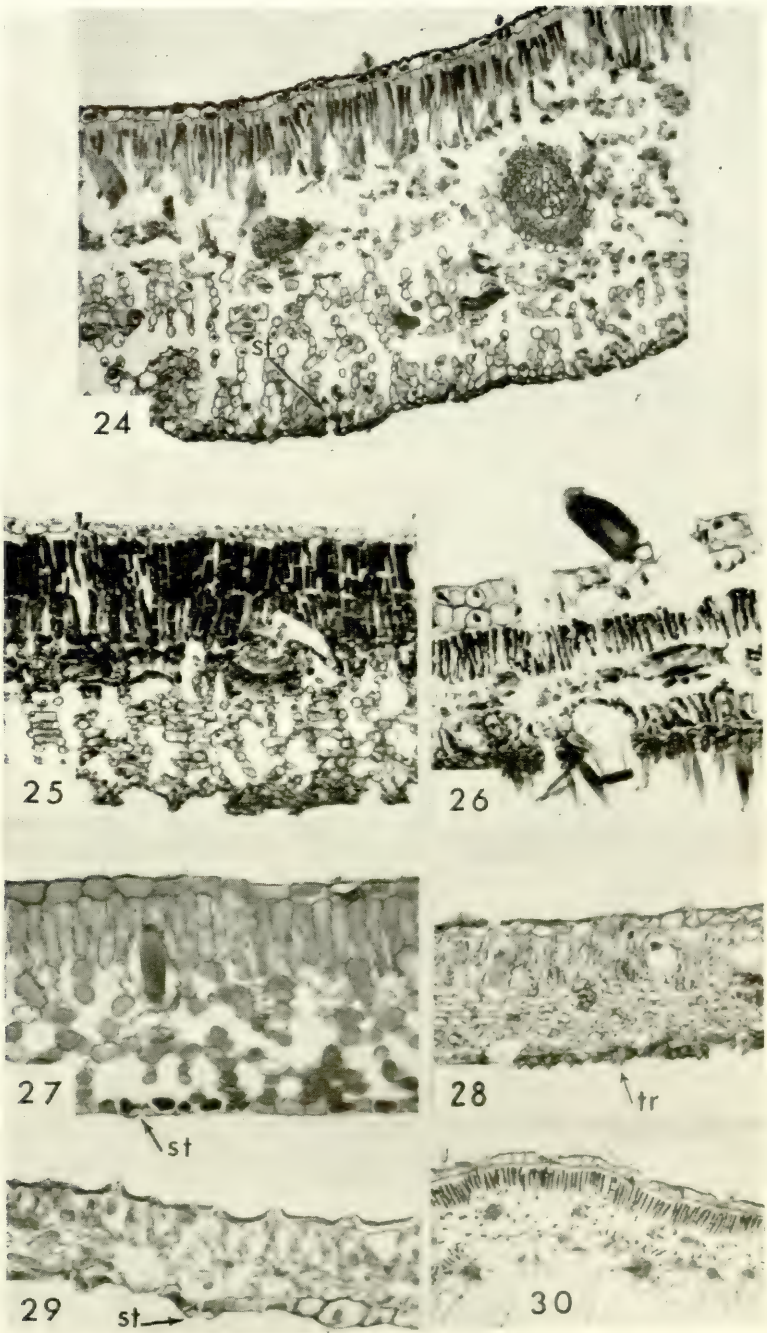

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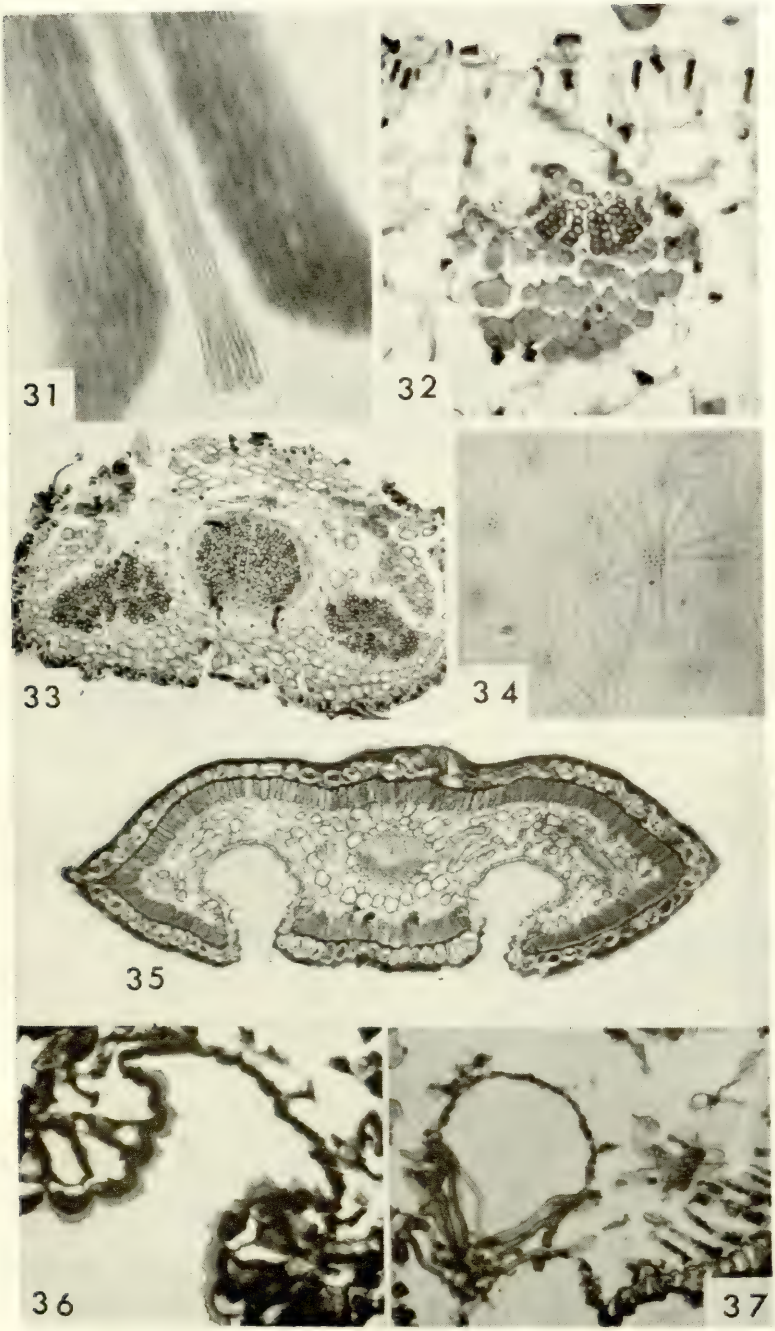

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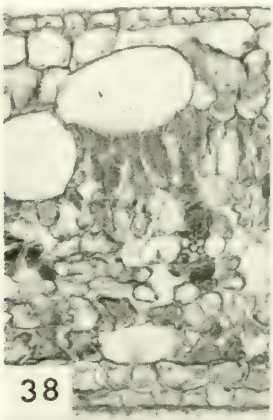

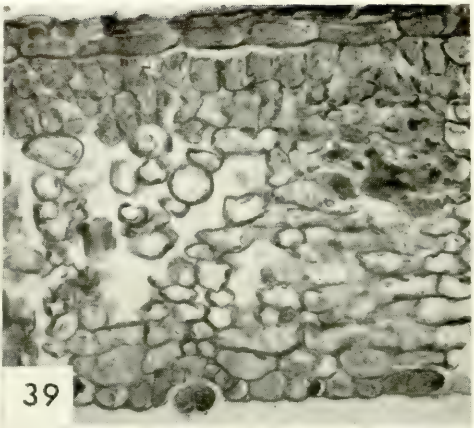

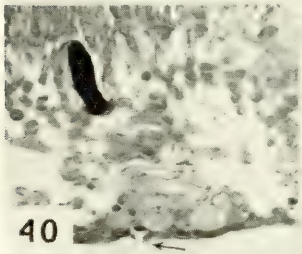

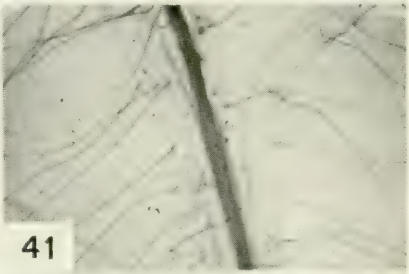

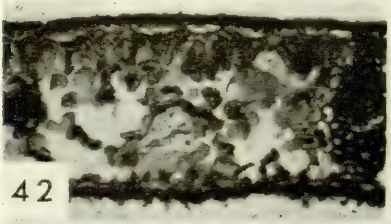

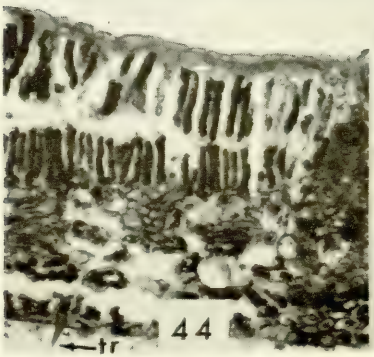

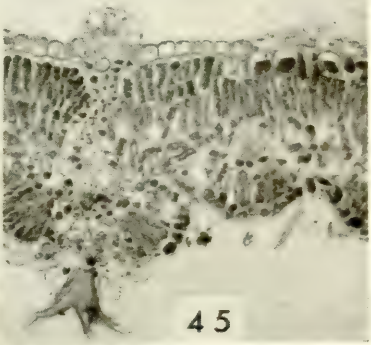

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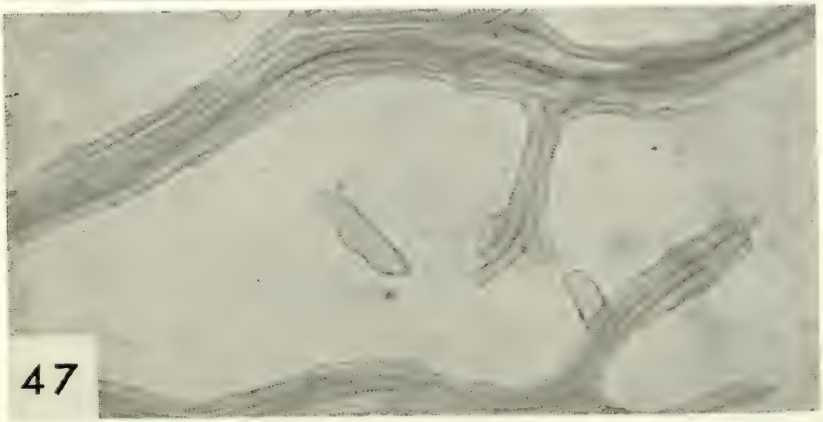
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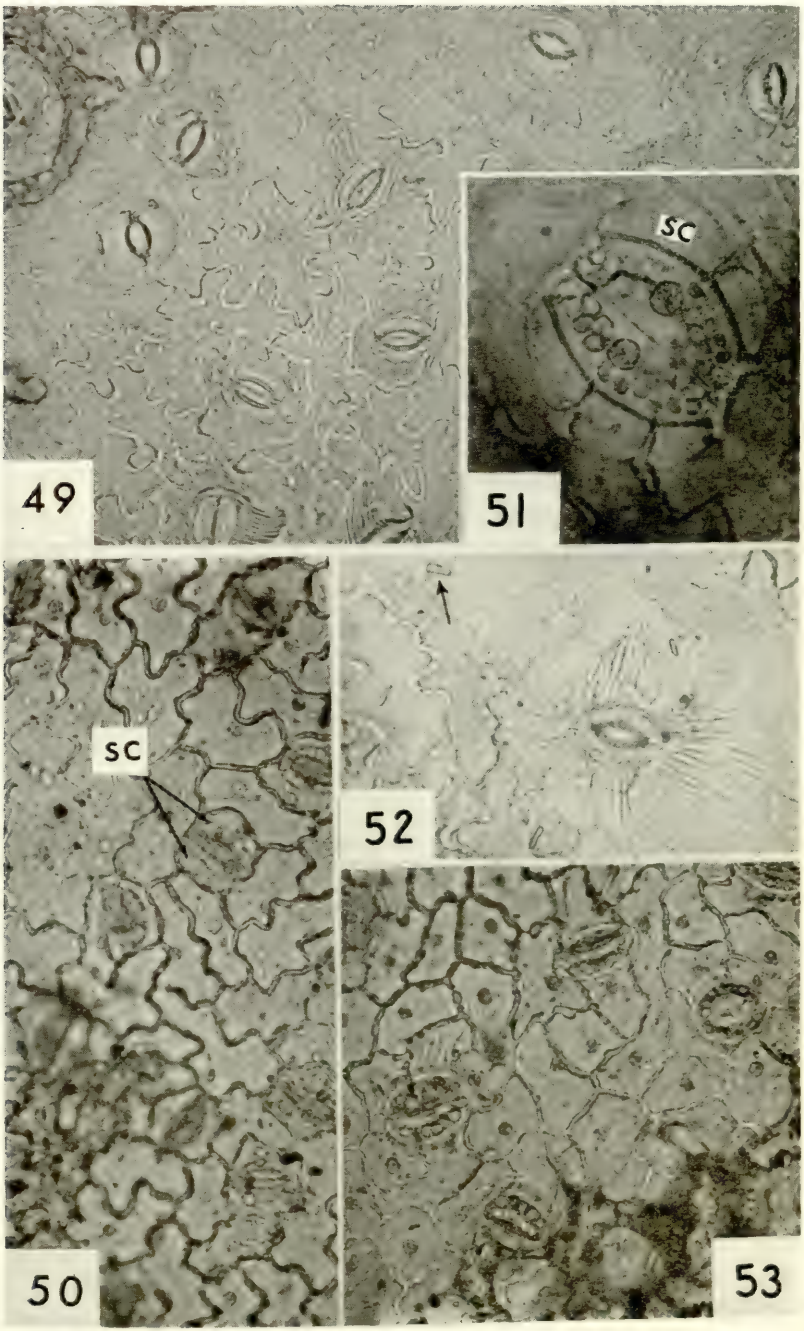

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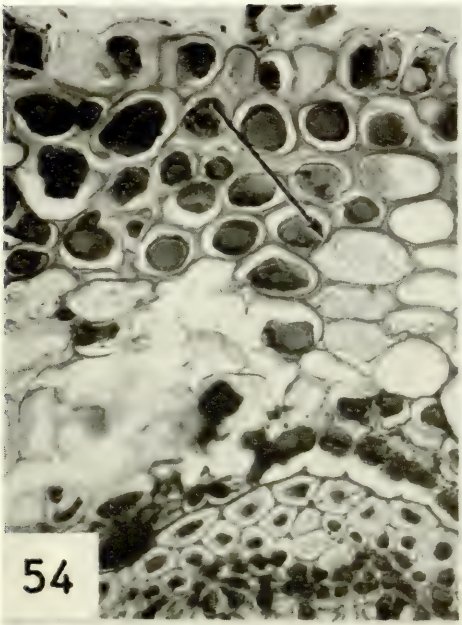

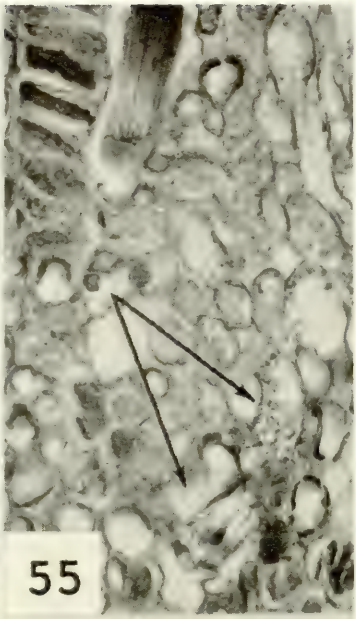

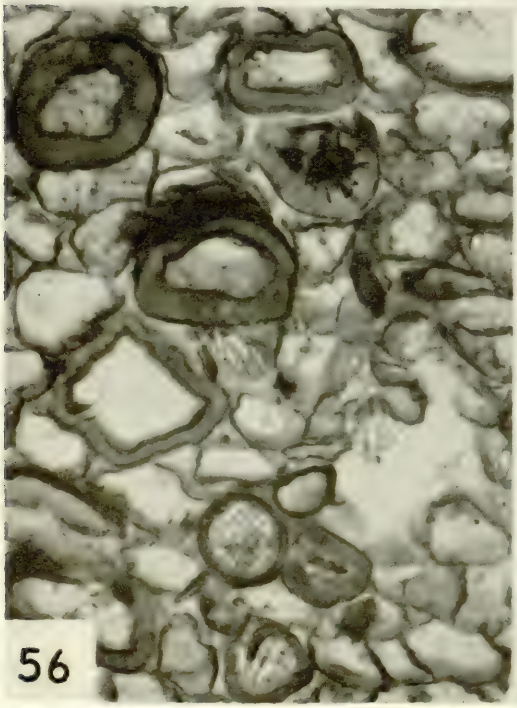

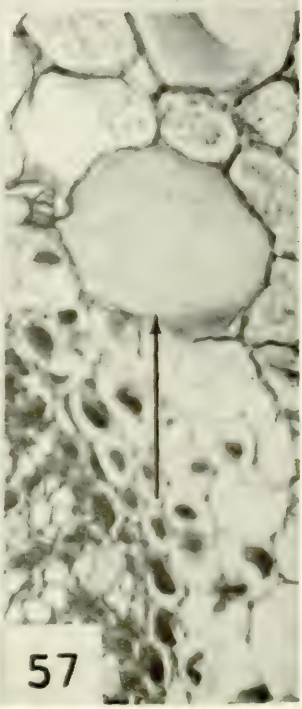

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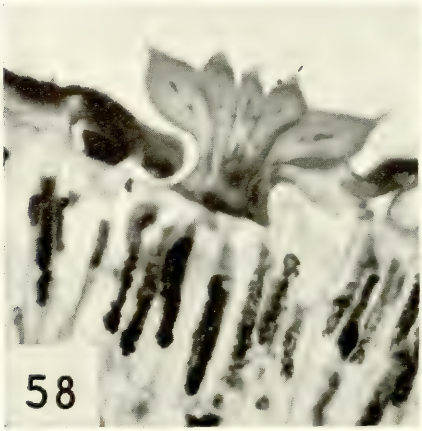

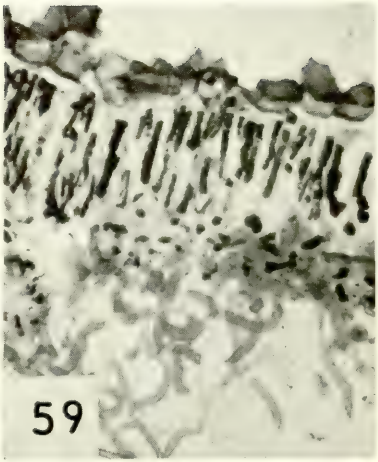

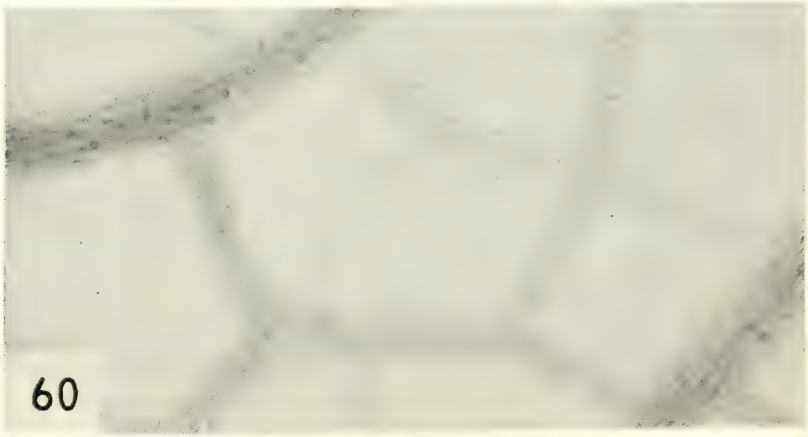

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THE MORPHOLOGY AND GERMINATION OF THE SEED OF ELEPHANTORRHIZA ELEPHANTINA

H. P. VAN DER SCHIJFF AND L. SNYMAN*

THE GENUS *Elephantorrhiza* Benth., described in 1842, belongs to the family Mimosaceae and consists, according to Phillips (1922, 1951), of only seven species with *Elephantorrhiza elephantina* (Burch.) S. Keels, the well known "elandsboontjie," as the type species. All the representatives of the genus are small shrubs that vary in height from about one foot, as in *E. elephantina*, to small trees of ten feet and higher in *E. burkei* Benth.

These plants are interesting in that they have thickened underground bases. It is a feature that generally occurs and is known in the Monocotyledoneae, but which is probably relatively rare in the Dicotyledoneae. However, this characteristic occurs in more South African Dicotyledoneae than is generally realized. Neither is it limited to a single or a few families, but it is found in a variety of families. The genera *Talinum* (Portulacaceae), *Gyrocarpus* (Hernandiaceae), *Elephantorrhiza* (Mimosaceae), *Bauhinia* (Caesalpinaceae), *Neorautanenia*, *Dolichos*, *Mucuna*, and *Erythrina* (Papilionaceae), *Rhoicissus* and *Cissus* (Vitaceae), *Adenia* (Passifloraceae), *Begonia* (Begoniaceae), *Cussonia* (Araliaceae), *Adenium* and *Pachypodium* (Apocynaceae), *Raphionacme* and *Ceropegia* (Asclepiadaceae), *Ipomoea* (Convolvulaceae), *Pterodiscus*, *Harpagophytum*, and *Sesamothamnus* (Pedaliaceae), and *Coccinia* (Curcurbitaceae) are particularly important in this respect.

Knowledge of the morphological character and development of these thickened bases is to a large extent still only speculative, while little is known of the morphology and germination of the seed. The aim of this study is an attempt to gain a better insight into the morphology and germination of the seed and the establishment of the seedling, the latter being very interesting and unusual for the Dicotyledoneae.

MATERIAL AND METHODS

The plant which we studied, *Elephantorrhiza elephantina*, is a small shrub up to 2 feet high (FIGURE 1) of which the underground parts are perennial while the stems above the ground partially or wholly die down annually during winter.

The leaves are bipinnately compound and the inflorescence consists of

* Most of this work was done while the senior author was a Mercer Research Fellow at the Arnold Arboretum, Harvard University, and was supported by a grant from the C.S.I.R., Republic of South Africa.

FIGURE 1. Single *Elephantorrhiza elephantina* plant to show bipinnately compound leaves and inflorescence.

small cream-colored flowers in a spike-like cluster that is up to 3 inches long. Although the ripe fruit is fairly hard, it readily absorbs water and disintegrates completely when wet, as a result of the softening of the pericarp flaps that break away from the remaining seams. It has been observed in the veld, that a large percentage of the seeds germinate on the surface of the soil within these moist, disintegrating fruits. At this stage it is not yet clear whether this is the ideal condition for the germination of the seeds.

The fleshy underground parts are very rich in tannic acid, a substance which is not only of medicinal value, but is also used in the tanning of hides. According to MacOwen (1897) an extract of the fleshy parts is used to treat sunburn, while Bryant (1909) maintains that the core of the "root" is used by Zulus as a cure for dysentery and diarrhoea. Thonner (1915) states that it is used as a fish poison and as a medicine, while it is known that an extract of the fleshy "roots" is an effective remedy for haemorrhoids.

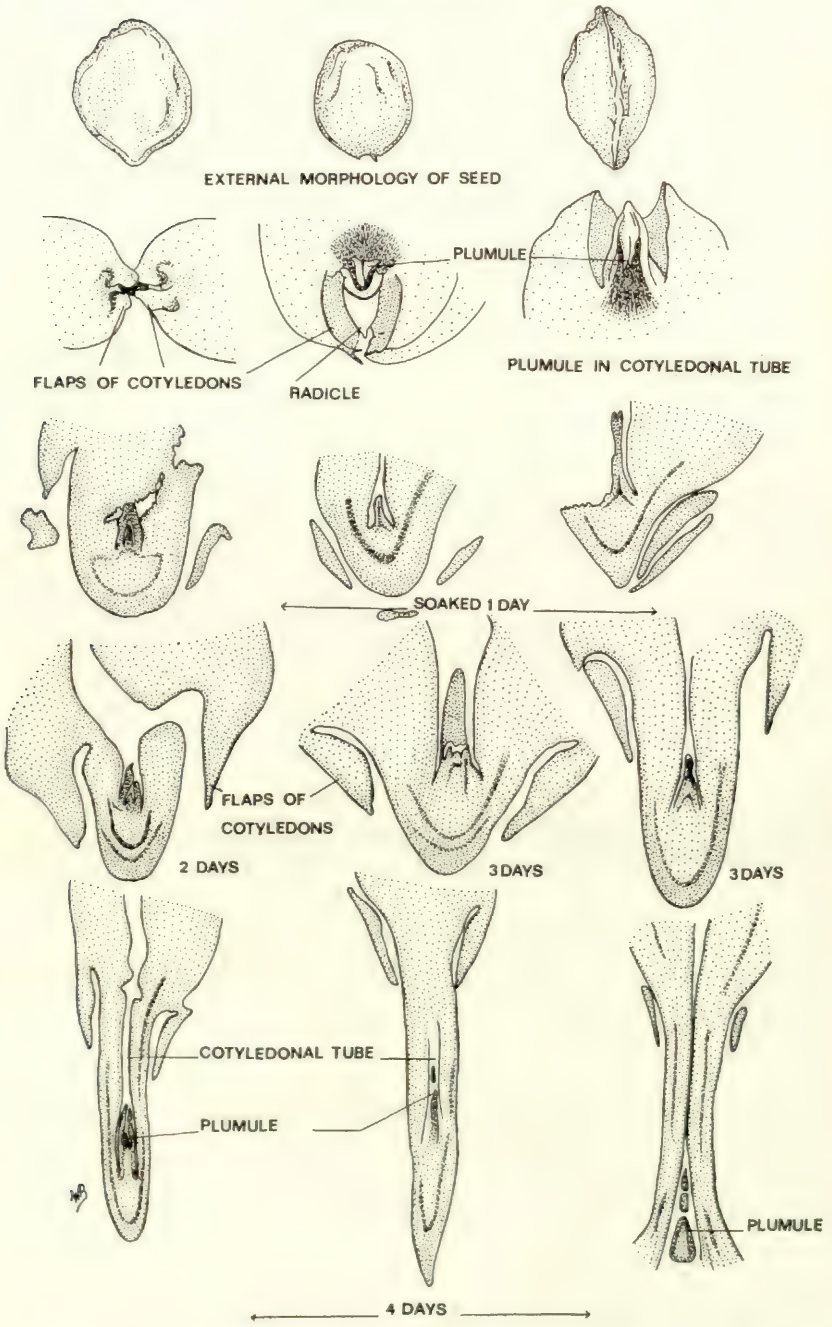
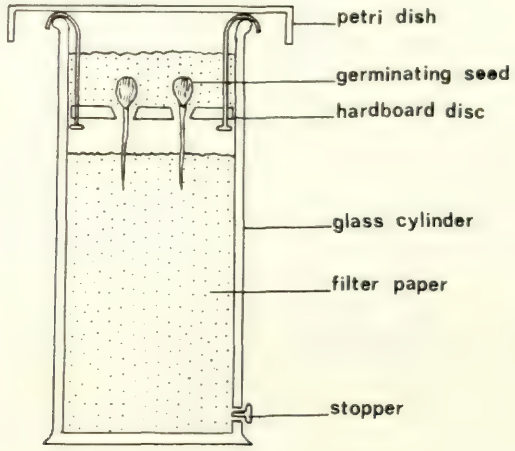


FIGURE 2. Drawings to illustrate seed morphology and the elongation of the cotyledon (petiole) tube during germination.

Steyn (1949) is not in agreement with Burtt-Davy that the plant is not toxic and is of the opinion that the seed contains an irritant toxin, which is harmful to animals.

Elephantorrhiza elephantina occurs fairly generally in the Eastern Cape Province, the Orange Free State, Natal, Transvaal, South West Africa,



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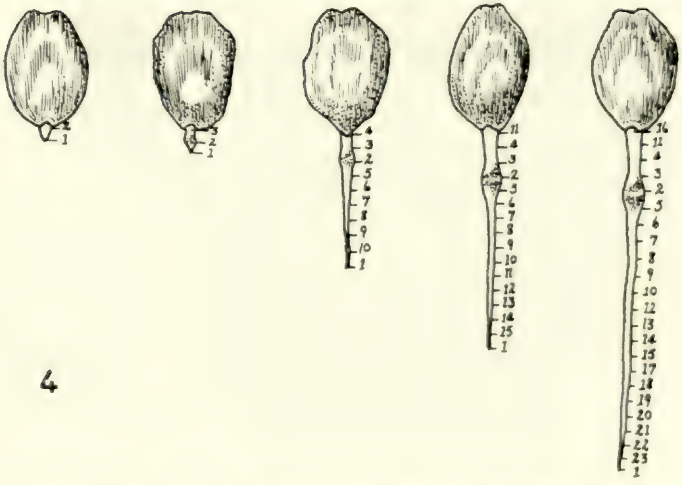

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FIGURES 3 AND 4. FIG. 3. Apparatus used to investigate the mode of germination of the seeds. FIG. 4. Diagrammatic representation of the elongation of the cotyledon (petiole) tube and "taproot" during germination.

Rhodesia, and Portuguese East Africa. In parts of the Transvaal highveld during spring it is often very common in veld which has been burned.

The seeds used in this investigation were collected in the vicinity of Pretoria, where the plant occurs fairly frequently in grassveld.

For the study of the morphology of the seed, dry seeds as well as seeds that had been soaked overnight were used. After drawings of the different seed forms were made (FIGURE 2) the hard leathery testa was carefully removed in order to study and to make drawings of the embryo, which is very brittle when dry.

Most of the material used for microtome sections was prepared according to standard methods and cast in wax. In some instances the material was fixed in acrolin, treated according to the method of Feder (unpubl.) and embedded in methacrylate resin. Although the latter method is more effective for the preparation of very thin sections, it is disadvantageous in that no serial sections can be made.

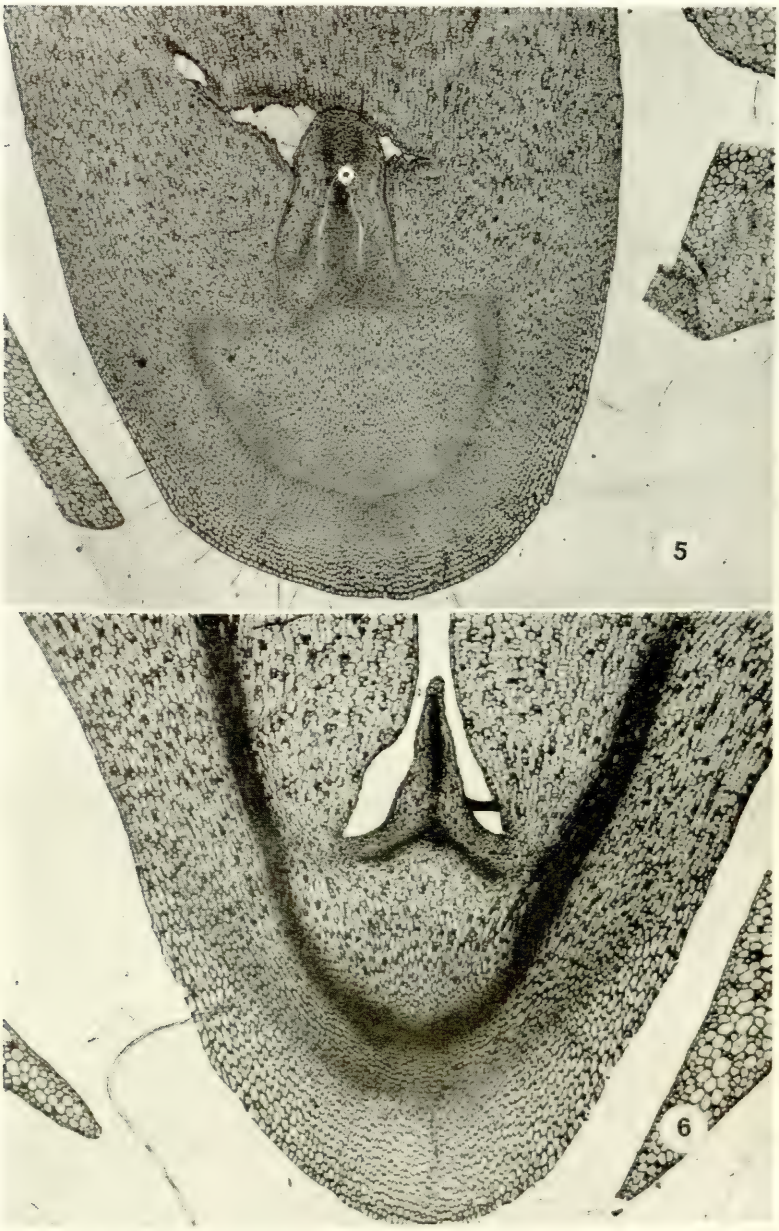
The seeds used in the germination tests and for the study of the seedlings were first wounded with a small knife to make an opening in the testa for moisture to penetrate the seed. They were then soaked overnight, after which they were placed on wet filter paper in petri dishes and left to germinate at a room temperature of about 25° C. In cases where the development of the seedling was followed, the seed was germinated in pure vermiculite in glazed pots about 18 inches high. The young seedlings, of which specimens were removed daily to be studied, fixed, and to be used in the making of drawings, were easily washed out of the vermiculite by means of a slow stream of water.

To trace the locality of elongation of the seedlings, germinated seeds were placed in holes made in a hardboard disc, which fitted into a glass cylinder impermeable to light. This was filled with moist crumpled filter paper and care was taken throughout to ensure that the roots did not come into contact with it (FIGURE 3).

The pattern of elongation of the axis of the seedling was traced by means of Indian ink markings, 1 mm. apart on the developing seedlings (Miller & Wetmore, 1945). The first mark was made on the tip of the radicle immediately after its appearance at the micropyle. Thereafter, serial marks were made on the elongating seedling axis and schematic and numerical drawings were made on a piece of paper. Where serial marks moved farther apart, new marks were made in between to show the precise region of elongation (FIGURE 4).

RESULTS

Morphology of the seed. The seeds of *Elephantorrhiza elephantina* (FIGURE 2) exhibit a wide variation in regard to size and form. However, the majority of the seeds are spherically flattened, being slightly tapered in the region of the micropyle. Some of the seeds are also tapered on the side opposite the micropyle. If the seeds are densely packed to-



FIGURES 5 and 6. FIG. 5. Longitudinal section through the base of embryo to show the position of the radicle and plumule. FIG. 6. Longitudinal section through base of seed during initial stages of germination to show the plumule in the still very short cotyledon (petiole) tube.

gether in the pods, they are flattened laterally. The seeds which are relatively large are up to 2 cm. broad and 2.5 cm. long.

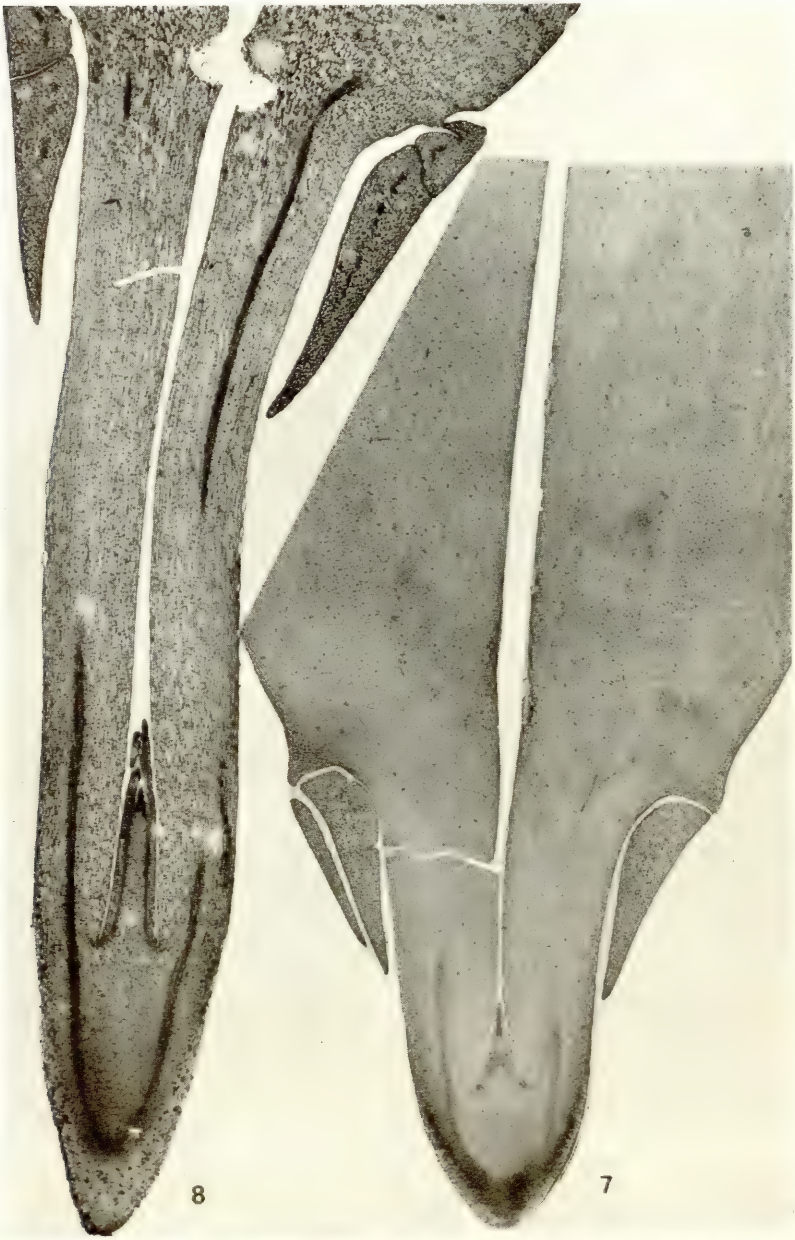
The embryo is surrounded by a hard leathery testa and the two thick and fleshy cotyledons are very brittle and are easily broken in the dry condition. They lie close together to protect the radicle and plumule between them. The cotyledons are oval in outline and asymmetrical at the base. Each cotyledon has two flaps at its base that fold over one another and protect the relatively large radicle (FIGURE 2). The cotyledons have short petioles which are fused to form a cotyledon tube or cylinder which surrounds the plumule and protects it (FIGURES 5–10). In the fusion area between the cotyledon tube and hypocotyl there are indications of meristematic tissue (intercalary meristem) which, together with cell elongation, is responsible for the elongation of the cotyledon tube during germination (FIGURES 6–8).

Germination of the seed. During the epigeal germination which usually occurs while the seed lies on the surface of the soil, the cotyledon flaps move apart and the radicle is forced out through the micropyle. According to the results obtained from the seedlings marked with Indian ink, it is clear that it is initially the cotyledon tube which elongates to carry the radicle out and that the apical growth of the radical only begins one or two days after germination has started (FIGURE 4). Root growth is fairly rapid and after one week tap roots of up to 9 inches in length were recorded.

Longitudinal sections of the embryo confirmed without question that the cotyledon tube elongates not only to carry the radicle out, but also to implant the plumule into the ground (FIGURES 6–8). These sections also clearly show the meristematic zone as well as the cylindrical form of the cotyledon tube. In cross section it can be seen that the tube in the earlier stages of germination is flattened (FIGURE 9) but later becomes cylindrical as can be seen in FIGURE 10. Under favorable conditions this cotyledon tube may be up to 4 cm. long, which is probably of particular ecological importance as it apparently ensures that the seedling becomes established deeply enough.

The plumule at first develops more slowly than the radicle. Between two to three weeks elapse from the time the radicle appears until the plumule becomes visible. It breaks through the cotyledon tube at the point of fusion between the cotyledon tube and the hypocotyl (FIGURE 11). At this stage the "root" has already undergone considerable secondary thickening and has formed a conspicuous loose periderm which peels off in brown flakes (FIGURE 13). The first sign of secondary thickening of the "root" (hypocotyl) is already visible three days after the radicle makes its appearance. No lateral roots were found on the upper and thickest part of the "root," while many lateral roots were present lower down (FIGURE 13).

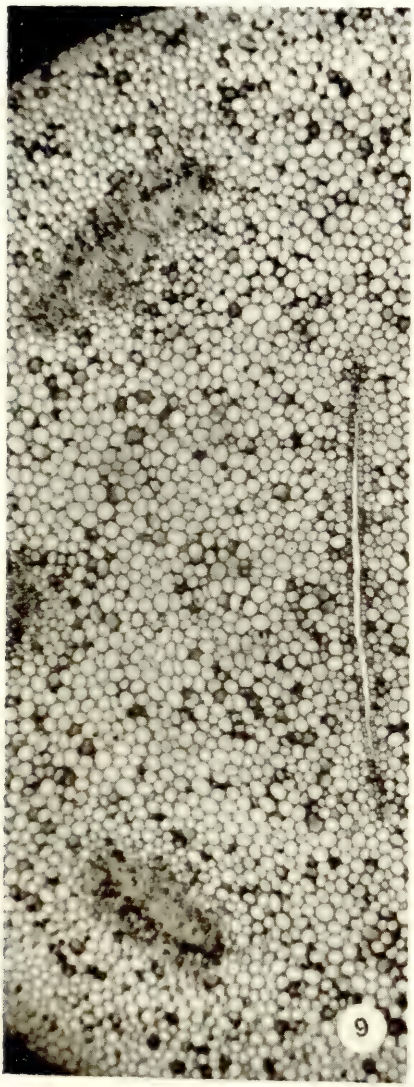
Each cotyledon stalk has three collateral vascular bundles (FIGURE 11). It is interesting to note that these bundles in the petioles of the cotyledons undergo secondary thickening, and also form a periderm (FIGURE 12).

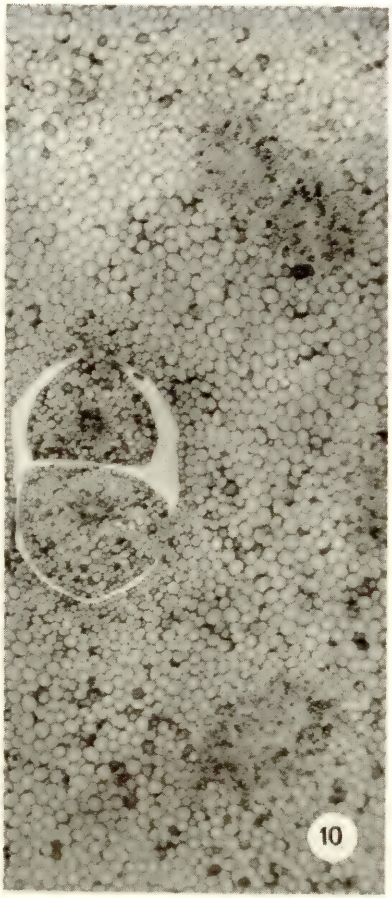


FIGURES 7 and 8. FIG. 7. Longitudinal section through embryo to illustrate elongation of petiole tube. FIG. 8. Longitudinal section of petiole tube of about 2 cm. length.

DISCUSSION

The type of germination encountered in *Elephantorrhiza elephantina* is not only very interesting, but also extraordinary for a representative of the Dicotyledoneae. It is the characteristic type of germination of representatives of the Monocotyledoneae, of which species of the South





FIGURES 9 and 10. FIG. 9. Transverse section through petiole tube to illustrate the three vascular bundles of each petiole and the flattened petiole cavity. FIG. 10. Transverse section through cylindrical petiole tube with young stem and leaf.

African genera *Phoenix*, *Jubaea*, and *Hyphaene* are probably the most important and most conspicuous. In these genera the radicle and plumule, as in the case of *Elephantorrhiza elephantina*, are also carried out by a cotyledon tube and down into the ground, the plumule bursting through the cotyledon tube some time after the radicle has made its appearance through the micropyle. The germination of the seed of *Elephantorrhiza elephantina* is also interesting in that the cotyledons remain within the testa, a feature which not only agrees with what is found in the Monocotyledoneae, but which is also characteristic of certain representatives of the order Policarpicae (Ranales) such as *Jeffersonia diphylla* (Berberidaceae), *Ranunculus* spp., and *Eranthis* spp. (Ranunculaceae) (Wettstein, 1962). In these Dicotyledoneae which exhibit some relationships with certain Monocotyledoneae, the radicle and plumule are also carried out by the elongating cotyledon stalks.

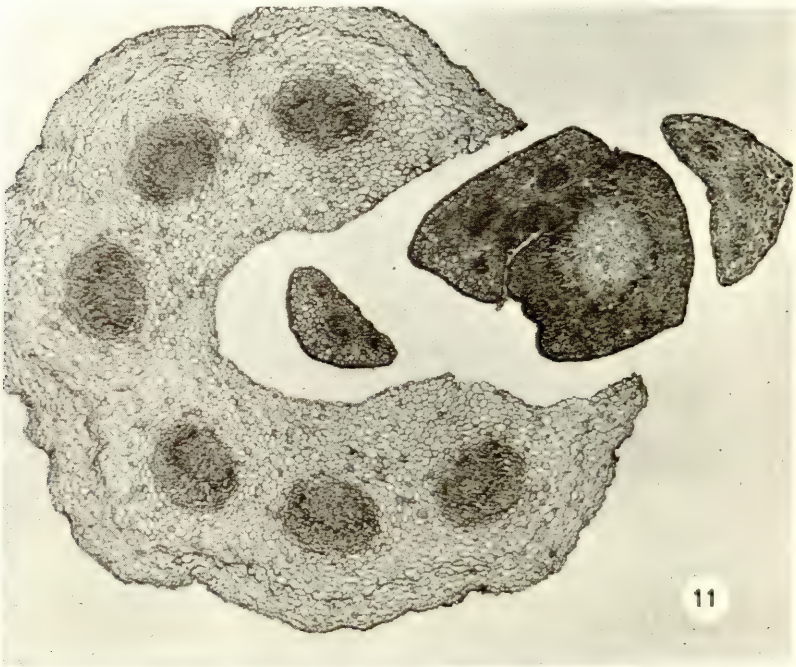


FIGURE 11. Transverse section through petiole tube and young plumule at the stage when the plumule breaks through the tube.

The same type of germination is also observed in *Elephantorrhiza burkei*, and according to Hofmeyr (1921–22) it is encountered in a representative of the Cucurbitaceae. Asa Gray (Hofmeyr, 1921–22), in his *Structural Botany*, maintains that it occurs in the American species *Megarrhiza californica* of the Cucurbitaceae.

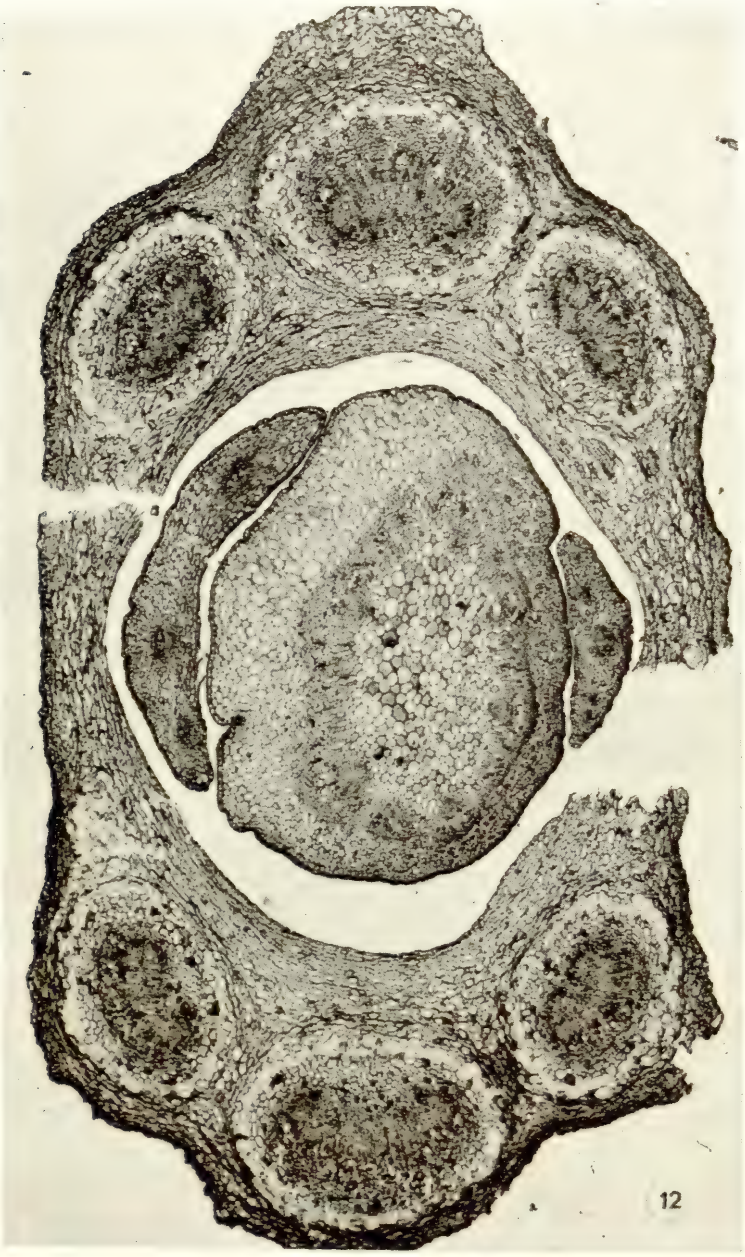


FIGURE 12. Transverse section through petiole tube and young stem to illustrate secondary thickening of the petiolar collateral vascular bundles.

Whether the germination of the seed and the development of the seedling of *Elephantorrhiza elephantina* is of any phylogenetic value is not clear. The phylogenetic importance of the germination morphology in the Polycarpicae can hardly be disputed, but here it appears as though it could be a case of convergence. Nevertheless, the facts that have been brought to light are most interesting and it can only be determined through further research how many of the South African plants exhibit this type of germination and whether it is of any phylogenetic significance.

SUMMARY

Elephantorrhiza elephantina the well known "elandsboontjie" of the family Mimosaceae is a small shrub of which the underground bases are thickened and fleshy.

The germination of the seed of this species is interesting in that the radicle and plumule are carried out by the cotyledon petioles which elongate and which are fused to form a cotyledon tube. This cotyledon tube can be up to 4 cm. long and probably contributes to the successful establishment of the seedling.

The elongation of the cotyledon tube is the result of cell elongation, and probably an intercalary meristem which is situated at the base of the cotyledons.

The tap root develops very rapidly, while the main stem breaks through the cotyledon tube about two weeks after the radicle has made its appearance.

Although this type of germination is characteristic of certain Monocotyledoneae and the cotyledon petiole of certain of the representatives of the Polycarpicae also elongate during germination, evidence is as yet incomplete to evaluate the phylogenetic importance thereof. As far as our present knowledge goes it appears as though it may be a case of convergence.

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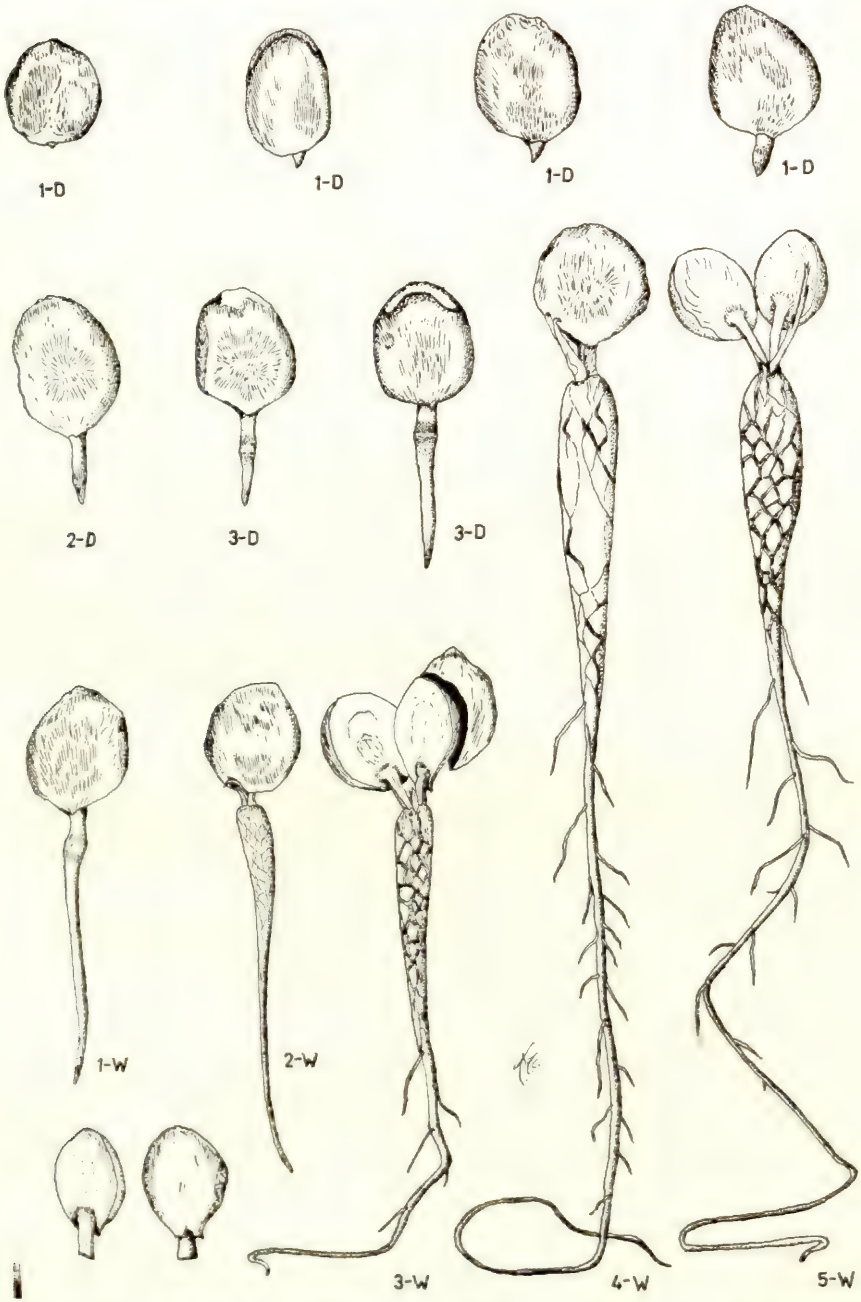

FIGURE 13, a and b. Different stages in the germination of the seeds and the development of the seedlings to illustrate secondary thickening of the "tap root" and lateral root development.

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7-W

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A NEW SPECIES OF ORMOSIA FROM BRAZIL

G. P. YAKOVLEV

WHILE STUDYING some unidentified material of South American *Ormosia* in the herbarium of the Komarov Botanical Institute, two specimens of a collection made by Riedel and Luschnath interested me greatly. These proved to represent an undescribed species which, according to the detailed and thorough treatment of Dr. Velva E. Rudd, is most closely related to *Ormosia friburgensis* Taub. ex. Harms, but differs from that species in many characters, as cited below. It agrees with *O. friburgensis* in having large yellow seeds (FIG. 1) each with a brown spot,

FIG. 1. *Ormosia ruddiana*, seed, × 1.

a character which distinguishes both these species from the majority remaining which have red, blackish red, or black seeds.

I am pleased to name this species for Velva E. Rudd, Curator, Department of Botany, Smithsonian Institution, who is an authority on the Leguminosae.

Ormosia ruddiana Yakovlev, sp. nov. FIG. 2.

Ormosia friburgensi affinis; arbor ad 6 m. alta; ramuli novelli fulvo-velutini; folia 7–13-foliolata, axi 12–20 cm. longo, laminis ellipticis vel oblongis, apice et basi acutis, marginibus leviter revolutis, subcoriaceis, supra subnitidis et glabris, 8–13 cm. longis, 2.5–3.5 cm. latis; venis secundariis 8–10, fere parallelis, conspicuis; flores ignotae; fructus indehiscens, sublignosus, leviter rugosus, fulvo- vel ferrugineo-velutinus, 1-spermus, 4.5–6.5 cm. longus, 3–3.5 cm. latus, 2–2.5 cm. crassus; semina subglobosa, flava, vel brunneola vel brunnea macula notata, 22–25 mm. longa et lata, ca. 20 mm. crassa; hilo 7–8 mm. longo, 2.5–3 mm. lato.

Typus: Arbor 15–20 ped., mont. Iatocolum [1] [Itacolomi], *Riedel & Luschnath* [Iter Brasiliense 1831–35] *649* (holotypus, isotypus LE).

[1] This locality is presumably Itacolomi, a mountain southwest of Ouro Prêto in the state of Minas Gerais, Brazil.

FIG. 2. *Ormosia ruddiana*, photograph of portion of holotype (LE).

The two species, *Ormosia friburgensis* and *O. ruddiana*, differ in the characters listed here.

	O. FRIBURGENSIS	O. RUDDIANA
Leaf axis	7–12 cm. (including petiole)	12–20 cm. (excluding petiole)
Leaflets	2–8 × 1–3 cm.	8–13 × 2.5–3.5 cm.
Petiolules	1–2 mm.	3–4 mm.
Length of legume	2.5–4.5 cm.	4.5–6.5 cm.
Hilum	4–5 × 1–1.5 mm.	7–8 × 2.5–3 mm.

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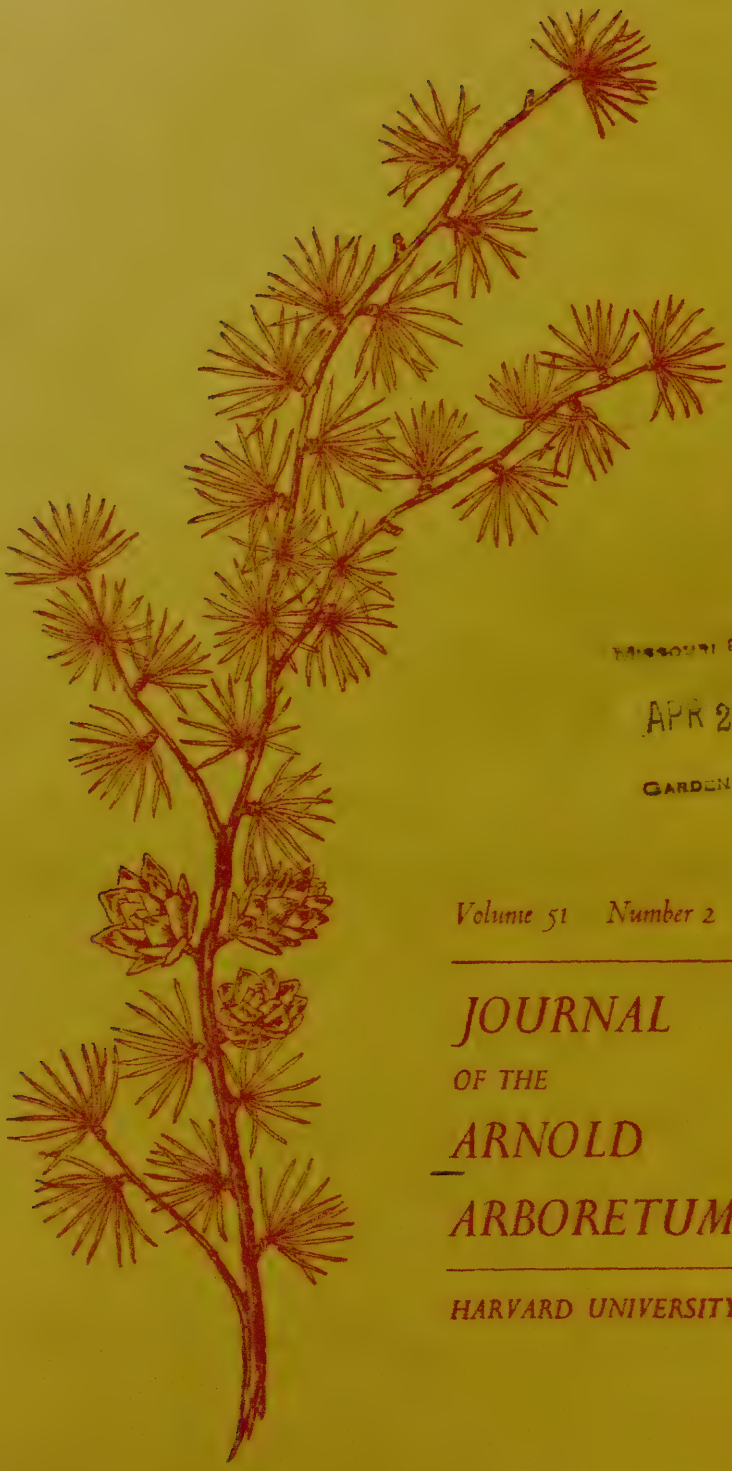

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COVER: The Golden Larch, *Pseudolarix* Gordon

WITH volume 51 the *Journal of the Arnold Arboretum* begins its second half century of continuous publication. To celebrate the occasion we are pleased to present a new cover format. The cover design is the work of Norman Comeau of the Art Department, Thomas Todd Company, Printers, Boston. We hope from time to time to have drawings of other plants on the cover. The Table of Contents will appear on the back cover. *Eds.*

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JOURNAL
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ARNOLD ARBORETUM

VOL. 51 APRIL 1970 NUMBER 2

A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR

S. M. A. KAZMI

THE TREATMENT OF THE BORAGINACEAE for Hooker's *Flora of British India* (4: 137–179. 1883) was prepared by C. B. Clarke. The area then comprised the present states of India, Pakistan, Kashmir, Nepal, Burma, and Ceylon. Many other authors have since contributed to the flora of West Pakistan and Kashmir but most of their publications are of regional nature or only enumerations of plants collected by them from different parts of the country.

Since C. B. Clarke's work no comprehensive revision of Boraginaceae of West Pakistan and Kashmir has been prepared. The additional information we have on this area is scattered in the following general works or in the revisions of this family for some of the adjoining areas.

In 1924 I. M. Johnston reviewed the Old World genera of the Boraginaceae, subfamily Boraginoideae (Contr. Gray Herb. 73: 42–73. 1924). His observations on some genera and species of our area appeared in scattered papers (Contr. Gray Herb. and Jour. Arnold Arb.) published between 1924 and 1957. Brand, from 1921 to 1931 (in Engler, Pflanzenreich IV. 252 (Heft 78): 1–183. 1921; IV. 252 (Heft 97): 1–236. 1931) revised several groups of Boraginaceae, including many genera and species from West Pakistan and Kashmir. Later the family was revised by Popov (Fl. URSS 19: 97–691. 1953). His revision is confined to the plants of URSS, but gives information on those species with distribution extended to West Pakistan and Kashmir.

Recently, H. Riedl (in Rechinger, Fl. Iranica 48: 1–266. 1967) dealt with the Boraginaceae of the Iranian Highlands, an area including the parts of West Pakistan westwards to the Indus; but the areas lying eastwards to the Indus and adjoining Kashmir and Jammu have been excluded as not being a part of the Iranian Highlands. His work is a valuable contribution to the study of Boraginaceae of West Pakistan as it gives the western limits of distribution of West Pakistan taxa and indicates their relationship with allied species of westerly distribution.

In the present paper an attempt has been made to revise the Borag-

inaceae of West Pakistan, east and west of the Indus and the whole State of Jammu and Kashmir, with a special interest in determining the eastern limits of distribution of the taxa of this area and their eastern relatives.

This revision is the result of a critical examination of the material accumulated at the Herbaria of the Arnold Arboretum and Gray Herbarium of Harvard University, including most of the collections of Stewart, Koelz, and Webster from India, Pakistan, and Kashmir and many other collections received from the Royal Botanic Gardens, Calcutta, the Forest Research Institute, Dehra Dun, and St. Xavier's College, Bombay, which were the object of studies of the late I. M. Johnston for over thirty years. My own collections, especially those made with Professor K. H. Rechinger and Miss J. Lamond in West Pakistan in 1965, which are preserved at the North Regional Laboratories, Peshawar, and the material I received on loan from other herbaria.

The following abbreviations[1] (from Lanjouw & Stafleu, Index Herbariorum, ed. 5) are used in the citation of specimens.

Arnold Arboretum (A)
British Museum (Natural History) (BM)
Royal Botanic Garden, Edinburgh (E)
Pakistan Forest Institute, Medicinal Plant Branch, Peshawar (PFI–M)
Conservatoire et Jardin Botaniques, Genève (G)
Gray Herbarium (GH)
Islamia College, Peshawar (ICP)
Karachi University (KAU)
Punjab University, Lahore (LAH)
University of Michigan, Ann Arbor (MICH)
North Regional Laboratories, Peshawar (PES)
Peshawar University (PEU)
Gordon College, Rawalpindi (RAW)
Naturhistorisches Museum, Wien (W)
U.S. National Museum, Washington, D.C. (US)

Other abbreviations, used in the citation of TYPE specimens, are also according to Lanjouw & Stafleu.

I am greatly obliged to Dr. Richard A. Howard, Director of the Arnold Arboretum, for the facilities of work provided for me at the Harvard University Herbaria under a Mercer Research Fellowship. I am also thankful for very courteous treatment, which I have received from the members of the staffs of the Arnold Arboretum and the Gray Herbarium. I am extremely indebted to Mr. B. L. Burtt of the Royal Botanic Garden, Edinburgh, and Dr. R. R. Stewart of the University of Michigan Herbarium for their encouragement, advice, and some very useful suggestions. I wish to express my thanks to Dr. Robert C. Foster for correcting my Latin diagnosis, to Dr. Bernice G. Schubert for making editorial corrections and to the Directors and Curators of the herbaria, who were kind enough to send material on loan for my studies.

[1] The symbols for the five herbaria in West Pakistan not included in Index Herbariorum, ed. 5, were suggested by Dr. F. A. Stafleu in a personal communication.

In the systematic account which follows, I have cited all the material I have examined. I have tried to arrange the collections in geographical sequence, grouping them under West Pakistan and Kashmir and their respective districts arranged alphabetically. The collections which, due to lack of information, could not be placed in any district, have been listed under Miscellaneous. I have not changed the spelling of the localities or the language of the collector's notes. In cases where the sheets were not numbered by collectors, I have given the herbarium number or any other indication, which might be useful in recognizing the sheet.

Boraginaceae Juss. Gen. Pl. 128. 1789 "Borragineae"

Syn.: *Boraginaceae* Lindl. Nat. Syst. ed. 2. 274. 1836; G. Don, Gen. Syst. 4: 306. 1838. *Asperifoliae* L. Ord. Nat. Pl. 489. 1792. *Asperifoliaceae* Reichenb. Conspect. Regni Veg. 118. 1828.

Herbs, shrubs or trees, usually scabrous, hispid hairy, sometimes glabrous. Leaves generally alternate, lowermost sometimes opposite, simple, usually entire, exstipulate. Inflorescence usually composed of 1 or more scorpioid or helicoid cymes that uncoil as the flowers open, or sometimes glomerate-racemose or spicate, sometimes loosely cymose or with solitary flowers, bracteolate or not. Flowers mostly bisexual, actinomorphic or rarely zygomorphic, hypogynous. Calyx usually regular, sometimes irregular, sepals 5, distinct or basally connate, imbricate or rarely valvate. Corolla 5-lobed, imbricate or contorted in bud, rotate, salverform, funnelform or campanulate; corolla tube with folds, sometimes terminated or partially closed by faucal appendages (scales). Stamens 5, epipetalous, equal or less commonly unequal, alternating with corolla lobes; anthers 2-celled, dehiscing longitudinally, basifixed or basally dorsifixed, introrse; annular nectariferous disc present or absent. Ovary superior, bilocular but becoming 4-locular at maturity; ovules anatropous or hemitropous; style terminal or gynobasic, long or short; stigma capitate or 2-lobed or sometimes style twice bifid. Fruit drupaceous or dividing into two bilocular or 4 unilocular (or one 4-locular) nutlets; seeds erect or oblique, testa membranous, albumen fleshy, embryo curved, radical superior.

A family of wide distribution, composed of about 100 genera and 2,000 species. About 60 genera are represented in the Old World including 36 in West Pakistan and Kashmir.

Key to the Genera

1. Trees or shrubs.
   2. Style 4-fid. ..... 1. *Cordia.*
   2. Style 2-fid. ..... 2. *Ehretia.*
1. Herbs, annual, biennial or perennial, rarely undershrubs.
   3. Style terminal on the entire ovary, not inserted between the carpels.
      4. Styles 2. ..... 3. *Coldenia.*
      4. Style 1 (to bifid). ..... 4. *Heliotropium.*

3. Style arising from between the carpels.
   5. Ovules 2, always 2 nutlets developed. . . . . 18. *Rochelia.*
   5. Ovules 4, nutlets 4 at least when immature, rarely 1–3 abortive (but at younger stage always 4).
      6. Apices of anthers subulate and contorted. . . . . 30. *Trichodesma.*
      6. Apices of anthers obtuse or apiculate, not subulate or contorted.
         7. Anthers strongly heteromorphic, the upper ones several times longer than the lower. . . . . 31. *Caccinia.*
         7. Anthers homomorphic, all of equal size.
            8. Faucal appendages (scales) absent, corolla throat sometimes villous, corolla tube usually longitudinally plicate.
               9. Anther connectives elongated, sterile; corolla lobes reduced to teeth. . . . . 29. *Onosma.*
               9. Anther connectives not elongated; corolla lobes distinct.
                  10. Gynobase elevated, pyramidal, more than half the length of the nutlets (corolla in W. Pakistan species strongly zygomorphic). . . . . 7. *Echiochilon.*
                  10. Gynobase plane; corolla actinomorphic.
                     11. Corolla throat densely filled with hairs; style undivided, stigma 1. . . . . 5. *Sericostoma.*
                     11. Corolla throat naked, sometimes gibbous; style divided, stigma 2–4.
                        12. Corolla throat glabrous, never gibbous; style 2–4-fid, rarely undivided; stigmas 2–4. . . . . 28. *Arnebia.*
                        12. Corolla throat gibbous; style 2-fid, stigmas 2. . . . . 27. *Lithospermum.*
            8. Faucal appendages (scales) present, sometimes represented only by hairs or minute glands (except in *P. parviflora* and *P. echioides*).
               13. Appendages 10, in two tiers, 5 alternating with the corolla lobes, the other 5 alternating with the stamens in the corolla tube. . . . . 34. *Decalipidanthus.*
               13. Appendages 5, in one tier, alternating with the stamens or corolla lobes in the corolla throat.
                  14. Nutlets neither glochidiate-appendiculate nor prickly, smooth, granulate, verruculose, tuberculate or variously rugulose, glabrous or hirtulous.
                     15. Calyx irregular, divided to the middle, dentate between the lobes, much enlarged at fruiting, compressed, subbilabiate, lobes dentate or lobate. . . . . 19. *Asperugo.*
                     15. Calyx regular, lobes subequal, not dentate between the lobes, not much enlarged at fruiting, neither compressed nor bilabiate, lobes not dentate or lobate.
                        16. Faucal appendages velvety or fimbriate, areola of nutlet prominently hollowed out by a thickened girdle. . . . . 33. *Nonea.*
                        16. Faucal appendages usually glabrous or puberulous, never fimbriate, areola of nutlet various.

17. Areola of nutlet concave with distinct smooth or slightly dentate but not thickened girdle.
    18. Areola of nutlet basal, if subventral corolla tube geniculate. ..... 32. *Anchusa*.
    18. Areola of nutlet ventral; corolla tube always erect. .... 35. *Gastrocotyle*.
17. Areola of nutlet neither concave nor girdled.
    19. Lower flowers distant, axillary, upper flowers in foliate spikes; corolla sinuate, tubular; areola basal, rims thick, ventrally developed. .. 6. *Bothriospermum*.
    19. Flowers never axillary; inflorescence bracteate or ebracteate; corolla various; areola without rim or collar.
        20. Areola of nutlet affixed subventrally to the gynobase. ..... 11. *Lasiocaryum*.
        20. Areola of nutlet affixed ventrally, suprabasally or medially to the gynobase.
            21. Corolla salverform, throat not differentiated, tube usually shorter than the calyx lobes; nutlets usually rough, attached ventrally, suprabasally or medially. .... 9. *Anoplocaryum*.
            21. Corolla tubular with well developed campanulate or funnelformed throat, tube usually surpassing the calyx lobes; nutlets usually smooth, attached basally or suprabasally.
                22. Corolla deep purple-blue, lobes at most equalling the tube, usually shorter; nutlets keeled. ..... 8. *Pseudomertensia*.

22. Corolla sky-blue to white, lobes at least equalling the tube, usually longer; nutlets not to scarcely keeled. . . . . 36. *Myosotis*.

14. Nutlets at the margin and in the middle area glochidiate-appendiculate, usually winged (in *Lappula* sometimes reduced to tubercles or prickles).
23. Gynobase flat; nutlets regularly tetrahedral, attached at one corner. . . . . 14. *Trigonotis*.
23. Gynobase conical, pyramidal or subulate; nutlets not tetrahedral, variously attached.
24. Nutlets with an elongate total lateral attachment to the gynobase, commonly decurrent on style.
25. Wings of nutlets incurved, middle area partly covered. 21. *Paracaryum*.
25. Wings of nutlets not or rarely slightly incurved, middle area never covered. . . . . 22. *Mattiastrum*.
24. Nutlets variously attached to the gynobase, not decurrent on style.
26. Nutlets with straight or uncinate, unicellular hairs, never tuberculate nor with multicellular glochidiate appendages, rarely smooth and glabrous (but if so always with stamens included). . . . . 20. *Omphalodes*.
26. Nutlets with some or more multicellular glochidiate appendages or evidently tuberculate, rarely smooth and glabrous (but then with stamens always exserted).
27. Middle area of nutlet distinctly ovate, apex acute, inner face above areola keeled throughout its length. . . . . 16. *Lepechiniella*.
27. Middle area of nutlet if distinct, oblong-ovate, trapeziform to narrowly triangular, inner face above the areola not at all keeled throughout its length.
28. Nutlets inseparable from the gynobase, bases of the marginal glochidiate appendages usually confluent. . . . . 17. *Heterocaryum*.
28. Nutlets separable from the gynobase, bases of marginal

glochidiate appendages usually not confluent.

29. Nutlets globose, semiglobose or napiform.
    30. Filaments evidently longer than anthers, attached above faucal appendages, anthers and filaments exceeding the corolla. ..... 23. *Solenanthus.*
    30. Filaments equalling the anthers, not inserted above the faucal appendages, anthers included or rarely slightly exceeding the corolla.
        31. Nutlets with very few glochidiate appendages and with a well developed wide cartilaginous margin. ..... 26. *Actinocarya.*
        31. Nutlets with many glochidiate appendages, marginless or with a weakly developed margin, thick, and evidently formed by the basal fusion of the lateral appendages.
            32. Anthers at maximum 3 times longer than broad. ..... 25. *Cynoglossum.*
            32. Anthers often more than 3 times longer than broad. ..... 24. *Lindelofia.*
29. Nutlets more or less pyramidal to truncate-pyramidal-oblong.
    33. Nutlets about equalling the elongate gynobase, attached for nearly the whole length, (with rare exceptions) exceeded by style, margins of nutlets toothed or lacerate, frequently glochidiate-appendiculate. ..... 15. *Lappula.*
    33. Nutlets much surpassing the stout pyramidal gynobase, attached obliquely and supramedially by the deltoid or ovate areola, surpassing the style.
        34. Nutlets (some or all of each fruit) with a thick medial, dorsal, annulate crest. ..... 13. *Microula.*
        34. Nutlets with a circumdorsal, commonly lacerate or dentate margin.
            35. Fruiting calyx reflexed; rank tufted plants with broad herbaceous leaves. ..... 12. *Hackelia.*
            35. Fruiting calyx erect or ascending; low densely cespitose plants with small firm leaves. ..... 10. *Eritrichium.*

1. **Cordia** L. Sp. Pl. 190. 1753; Gen. Pl. ed. 5. 87. 1754

TYPE SPECIES: *C. myxa* L.

Trees or shrubs. Leaves small to large, usually evidently petiolate, margins entire, serrate, or rarely evenly lobulate. Inflorescence of ebracteate cymes, mostly corymbose. Flowers homomorphic, or heterostyled, or functionally more or less unisexual (functionally male flowers with style and stigmas much reduced or completely undeveloped); corolla campanulate to funnelform, small to large, white, yellow-orange or red, usually 5-merous but occasionally 4–8-merous, lobes ascending to recurved, tube short to long, cylindric or spreading; stamens exserted to included, filaments often hairy towards the base, usually well developed; style terminal on ovary, dichotomous, a simple column at base then dividing into 2 branches, which in turn fork to produce the 4 ultimate branches each bearing a stigma; stigmas 4, clavate to spathulate or capitate. Fruit a drupe with watery or glutinous mesocarp or rarely without fleshy

mesocarp and hence a nut; endocarp bony, 1–4-seeded. Seeds without endosperm.

About 250 species, mainly of the American tropics.

KEY TO THE SPECIES

a. Leaves once and a half to twice as long as broad.
  b. Corolla tube longer than corolla lobes, lobes ± 3 mm. long. ..... 1. *C. gharaf.*
  b. Corolla tube shorter than corolla lobes, lobes 5–6 mm. long. ..... 2. *C. dichotoma.*
a. Leaves less than one and a half times as long as broad, frequently as broad as long.
  c. Calyx not ribbed, glabrous externally. ..... 3. *C. obliqua.*
  c. Calyx ribbed, pubescent or tomentose externally.
    d. Leaves cordate or rounded at the base; corolla tube glabrous within. ..... 4. *C. macleodii.*
    d. Leaves cuneate or rounded at the base; corolla tube hairy within.
      e. Pedicel tomentose; calyx ± 10 mm. long. ..... 5. *C. vestita.*
      e. Pedicel subglabrous; calyx 3–4 mm. long. ..... 6. *C. myxa.*

1. **C. gharaf** (Forssk.) Ehren. ex Asch. Sitz-ber. Ges. Naturf. Freunde **1879**: 46. 1879; Verh. Bot. Ver. Brandenb. **21**(*2*): 69. 1880; Muschler, Man. Fl. Egypt **2**: 781. 1912.

Cornus gharaf Forssk. Fl. Aegypt.-Arab. xcv. 1775.
Cornus sanguinea Forssk. *Ibid.* 33. 1775, non L.
Cordia sinensis Lam. Encycl. Méth. Bot. **1**: 423. 1791; I. M. Johnston, Jour. Arnold Arb. **32**: 11. 1951.
Cordia rothii Roem. & Schult. Syst. Veg. **4**: 798. 1819; DC. Prodr. **9**: 480. 1845; Brandis, Forest Fl. India 338. 1874, Indian Trees 480. 1921; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 138. 1883; Cooke, Fl. Bombay Presidency **2**: 202. 1908; Parker, Forest Fl. Punjab 360. 1924; Riedl in Rechinger, Fl. Iranica **48**: 6. 1967.
Cordia angustifolia Roxb. Fl. Indica, ed. Carey & Wall. **2**: 338. 1824, non Roem. & Schult.
Cordia subopposita DC. Prodr. **9**: 480. 1845.

TYPE: Arabia: Hadie, *Forsskål, s.n.* (as *Cornus sanguinea* Forssk. C.)
ICON.: Brandis, Indian Trees *fig. 172.* 1921; Wight, Icon. Pl. Indiae Orient. **4**: *t.1379.* 1848, under *C. rothii* Roem. & Schult.

A large or small tree, twigs glabrous or nearly so. Leaves subopposite, 5–10 cm. long, 2–2.5 cm. broad, oblanceolate oblong, entire or undulate, apices usually rounded, rough and glabrous above when mature, more or less pubescent below; petioles 8–13 mm. long. Inflorescence short paniculate-corymbose, subtomentose; peduncles 1.2–2.5 cm. long, puberulous to subtomentose. Flowers 5 mm. across, white, usually tetramerous, pedicel short, slender. Calyx ± 5 mm. long, minutely pubescent externally, silky within, campanulate-tubular, lobes small, obtuse. Corolla tube equalling the calyx lobes, corolla lobes short, ± 3 mm. long, obtuse, reflexed, fila-

ments glabrous. Drupe usually 1-seeded, about 12 mm. long, ovoid, mucronate, striate, yellow or reddish brown when ripe.

DISTRIBUTION: Pakistan, India, Ceylon, Arabia, and North Africa.

West Pakistan: JHELUM DIST.: Langarpur, *R. R. Stewart 544* (K, RAW). KARACHI DIST.: Jemadar ka Landa near Karachi, *Stocks 427* (K); Karachi, *Jafri s.n.* (KAU). LAHORE DIST.: Lahore, *Thomson s.n.* (K), *R. R. Stewart s.n.* (K). Reported from Sind and Baluchistan.

Kashmir: Reported from Jammu.

Forsskål called the plant collected by him from Beit el Fakih and Hadie by its local name *Cornus gharaf*. This name has sometimes been rejected by many authors, most recently by Meikle (Israel Jour. Bot. **18**: 141, 142. 1969), as a *nomen nudum* because no description was given on page xci, xciii, xcv, xcvii, and xcix of Forsskål Fl. Aegypt.-Arab. 1775, but on page xcix there is a clear reference to the description under *Cornus sanguinea*.[2]

The epithet *sanguinea* was not available in the genus *Cornus* but could have been used by Ascherson for his new combination under *Cordia* instead of *gharaf*. However, since the name *gharaf* was selected by him, used later by many authors, and of course has no problems of priority, it should be accepted.

Cordia gharaf is said (Parker *l.c.*) to be wild in Jaipur State on the Delhi Ridge and probably also in the hills of southeast Punjab, and planted elsewhere.

2. **C. dichotoma** Forster, Prodr. 18. 1786.

Varrenia sinensis Lour. Pl. Cochinch. 138. 1790.
Cordia indica Lam. Encycl. Méth. Bot. **1**: 422. 1791.
Cordia lourieri Roem. & Schult. Syst. Veg. **4**: 466. 1819.
C. suaveolens Blume, Bijdr. Natuurk. Wetens. **14**: 843. 1826.
C. brownii DC. Prodr. **9**: 499. 1845.
C. ixiocarpa F. Muell. Frag. Phytogr. Austral. **1**: 59. 1856.
C. lowriana Brandis, Indian Trees 479. 1906.

TYPE: "New Caledonia" without citation of collector's name (BM).

Trees 3–10 m. tall. Leaves elliptic to ovate or obovate, usually 8–12 cm. long, 4–8 cm. broad, apices obtuse, base rounded to acute, margins entire to rarely sinuate above the middle, upper surface sparingly puberulent, glabrescent or at times dotted, lower surface paler, puberulent, usually glabrescent; petioles slender, 2–4 cm. long. Inflorescence cymose, dichotomous, bractless, loosely branched; peduncles 1–3 cm. long. Flowers of two sorts, male and hermaphrodite, produced, apparently, on separate trees. Male flowers shorter than the hermaphrodite, similar in form or at times with somewhat expanded corolla tube; filaments 3.5–4.7 mm. long, spar-

[2] On page xcix we find "Cornus gharaf. C. II. 10. In cephalagia." This refers to Centuria II, species no. 10 [on p. 33], which is *Cornus sanguinea*. Therefore, there is no doubt about what is meant by *Cornus gharaf* and *C. sanguinea*.

ingly hairy below the middle; anthers 2–2.8 mm. long; ovary abortive, globose, glabrous, bearing a minute terminal papilla representing the undeveloped style. Hermaphrodite flowers with calyx 5–6 mm. long, oblong in bud, not striate, campanulate, 4–6 mm. in diameter at summit, base rounded, sessile, lobes recurved, unequal, somewhat triangular; corolla 8–10 mm. long, lobes recurving, 5–6 mm. long, 2–2.5 mm. wide, tube 3–5 mm. long, usually shorter than the lobes, hairy only below the stamen-attachment; filaments 1–2 mm. long, sparingly hairy below the middle; styles with basal column 1–1.5 mm. long, the first branch about 1 mm. long, the ultimate stigmatiferous branches 3–6 mm. long, flattened, broadened, and not usually minutely lobulate above the middle. Drupe with viscous mesocarp, globose, 10–15 mm. in diameter, yellow or somewhat orange or reddish, supported by an accrescent indurate saucer-shaped calyx, 8–12 mm. in diameter.

DISTRIBUTION: Pakistan, Kashmir, India, southern China, Formosa, Hainan, Indochina, New Caledonia, and northeastern Australia.

West Pakistan: Reported from Karachi, Sind, Lower Baluchistan, Salt Range, Multan, and Rawalpindi, both wild and cultivated.

Kashmir: Reported from Mirpur, Billawar, and Jammu, both wild and cultivated.

The thinner more elongate, frequently acuminate leaves of *Cordia dichotoma* are usually once and a half to twice as long as broad, they are never subcordate at base as is frequently the case with the leaves of *C. myxa* and relatives. *Cordia myxa*, *C. obliqua* and their allies differ from *C. dichotoma* in their rounded thickish nonacuminate leaves, as well as in their coarser flowers, and very much larger drupes. Typically their leaves are less than once and a half as long as broad, frequently they are about as broad as long.

3. **C. obliqua** Willd. Phytogr. 1(4): *t. 4, fig. 1.* 1794. Willd., Linn. Sp. Pl. 1: 1072. 1797; DC. Prodr. 9: 479. 1845; C. B. Clarke in Hook. f. Fl. Brit. India 4: 137. 1883; Parker, Forest Fl. Punjab 359. 1924; Kashyap, Lahore Dist. Fl. 167. 1936.

C. latifolia Roxb. Fl. Indica, ed. Carey & Wall. 2: 330. 1824; Brandis, Forest Fl. India 336. 1874, *pro parte.*

TYPE: Habitat in Malabaria, *Klein, s.n.* (B).
ICON.: Willd. l.c. *t. 4. fig. 1.* 1794.

A medium-sized deciduous tree; bark with numerous shallow longitudinal fissures; branchlets glabrous or more or less brown-tomentose when young. Leaves 7–13 cm. long, 6–12 cm. broad, variable, orbicular, broadly ovate, elliptic or obovate, obtuse or more or less abruptly acuminate, base rounded, rarely cuneate, margins entire or slightly sinuate-dentate, glabrous or nearly so above but rather harsh, without white discs, more or

less pubescent, especially in the axils of the nerves beneath, basal nerves 3 rarely 5; petioles 17–35 mm. long. Inflorescence large, lax, of terminal or axillary pedunculate cymes; peduncles 2.5–5 mm. long. Flowers white, 5–10 mm. across, polygamous; pedicels short; buds pyriform. Calyx about 2.5 mm. long, glabrous externally or scarcely villous at the margins, pubescent within, splitting irregularly on the opening of the flower. Corolla tube as long as the calyx; lobes 5, as long as the tube, oblong-obtuse, recurved. Filaments hairy at base. Drupe ovoid, 12–25 mm. long, apiculate, yellowish brown, pink or nearly black when ripe, shining, minutely rugose, supported by the saucer-shaped, faintly striate calyx; pulp nearly transparent, viscid, sweetish, edible.

DISTRIBUTION: Pakistan, India, Ceylon (and North Africa ?).

3a. Var. **obliqua.**

Adult leaves glabrous beneath; calyx glabrous externally, scarcely villous on the margins.

West Pakistan: Reported from Rawalpindi and Salt Range, often cultivated.

3b. Var. **tomentosa** (Wall.) Kazmi, comb. nov.

C. tomentosa Wall. in Roxb. Fl. Indica, ed. Carey & Wall. **2:** 339. 1824.
C. wallichii G. Don, Gen. Syst. **4:** 379. 1838; DC. Prodr. **9:** 479. 1845; Cooke, Fl. Bombay Presidency **2:** 200. 1908; Brandis, Indian Trees 479. 1921.
C. obliqua var. *wallichii* (G. Don) C. B. Clarke in Hook. f. Fl. Brit. India **4:** 137. 1883.

TYPE: India in Dr. Heyne's collection, under *C. obliqua* var. (K).

Adult leaves densely stellate fulvous or white tomentose beneath; calyx glabrous externally.

West Pakistan: Lahore Dist.: Lahore, *Kazmi 2469* (PES).

C. myxa sensu C. B. Clarke in Hook. f. Fl. Brit. India **4:** 136. 1883, is a misidentification.

4. **C. macleodii** (Griff.) Hook. f. & Thoms. Jour. Linn. Soc. Bot. **2:** 128. 1858; C. B. Clarke in Hook. f. Fl. Brit. India **4:** 139. 1883; Brandis, Forest Fl. India 337. *t. 41.* 1874, Indian Trees 479. 1921; Cooke, Fl. Bombay Presidency **2:** 200. 1908; Parker, Forest Fl. Punjab 359. 1924.

Hemigymnia macleodii Griff. Calcutta Jour. Nat. Hist. **3:** 363. 1843.

TYPE: Sylvae Jubbulpore vicinae, plerumque cum *Tectona* consociata, Herb. Griff. (K).
ICON.: Brandis, l.c. *t. 41.* 1874.

A small tree with smooth gray bark, twigs clothed with dense white pubescence. Leaves alternate or sometimes almost subopposite, 7–18 cm. long, 5–15 cm. broad, orbicular or broadly ovate, obtuse, base cordate or

rounded, margins sinuate, firm and hard when mature, glabrous above with impressed nerves and raised discs, clothed beneath with short, dense, gray tomentum, basal nerves usually 3–5 or the nerves subbasal or sometimes the lowest pair of the secondary nerves arising at some distance from the base; petioles 2.5–5 cm. long, stout, tomentose. Inflorescence of terminal and axillary paniculate cymes, tomentose. Flowers white, 12 mm. across, subsessile, polygamous; buds obovoid. Calyx 6–8 mm. long, thick, ribbed, densely tomentose externally, glabrous within, lobes usually 6, as long or longer than the tube, spreading, spathulate-oblong, obtuse, veined. Filaments hairy at the base. Drupe 12–18 mm. long, ovoid, acute, supported by the cup-shaped, slightly ribbed calyx, not edible.

DISTRIBUTION: Pakistan and India.

West Pakistan: SIALKOT DIST.: Sialkot Proper (seeds collected from Sialkot and grown at Dehra Dun), *Ishtiaq Hussain s.n.* (GH). Cultivated eastwards to Rawalpindi.

5. **C. vestita** (DC.) Hook. f. & Thoms. Jour. Linn. Soc. Bot. **2**: 128. 1858; Brandis, Forest Fl. India 338. 1874, Indian Trees 480. 1921; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 139. 1883; Parker, Forest Fl. Punjab 38. 1924.

C. incana Royle, Illus. Bot. Himal. Mount. **1**: 306. 1839, *nomen nudum*.
Gynaion vestitum DC. Prodr. **9**: 468. 1845.

TYPE: In Himalaya occidentali tropica, Garhwal ad Pau, alt. 3,000–4,000 ped. *Edgeworth s.n.* (G–DC).

A small deciduous tree, bark greenish gray, exfoliating in large woody flakes, branchlets densely gray-tomentose when young. Leaves alternate, 7.5–15 cm. long, 6–13 cm. broad, sometimes larger, orbicular, broadly ovate or obovate, apices rounded or acuminate, base rounded or cuneate near the petioles, margins undulate, scabrous above with rather prominent white discs, tomentose beneath until mature, basal nerves 3–5, arising usually from a little above the base; petioles 2–4 cm. long, stout. Inflorescence of dense compound cymes, male in unilateral racemes; peduncles tomentose. Flowers yellowish white, 12 mm. across, polygamous; pedicels tomentose; buds pyriform. Calyx 10 mm. long, pubescent, more or less ribbed outside, slightly hairy near the base inside, lobes 5. Corolla tube equalling the calyx, very hairy within, lobes 5, slightly shorter than the tube, spreading, obovate, crenulate, notched at the tips. Filaments hairy at base. Drupe 1.7 cm. long, ellipsoid, acute, supported by the accrescent calyx, which is campanulate, 12 mm. long, thick and strongly ribbed; pulp gelatinous, edible.

DISTRIBUTION: Pakistan and India.

West Pakistan: SIALKOT DIST.: Mt. Tilla, *Aitchison 45* (K). Salt Range and Sub-Himalayan tracts, not common, often cultivated.
Kashmir: Reported from Mirpur and Jammu.

6. **C. myxa** L. Sp. Pl. 190. 1753; DC. Prodr. 9: 479. 1845; Cooke, Fl. Bombay Presidency 2: 200. 1908; Brandis, Forest Fl. India 366. 1874, excluding synonyms.

TYPE: "Habitat in Aegypto, Malabaria" *Herb. No. 253.1* (LINN).
ICON.: Wight, Illustr. Indian Bot. 2: *t. 169*. 1841.

A moderate-sized deciduous tree reaching about 13 m., or a large shrub; bark dark, rough, fissured; branchlets usually glabrous. Leaves alternate, broadly ovate to suborbicular, obtuse, ca. 5 cm. long and 4 cm. broad, entire or with slightly uneven undulate margins, upper surface glabrous, the lower pubescent. Inflorescence paniculate or paniculate-corymbose, usually subglabrous. Calyx 3–4 mm. long, campanulate-tubular, usually pubescent, lobes short. Corolla tube hairy inside, lobes 5, short, 2.5–3 mm. long. Fruits up to 18 mm. long, subacute, ovate.

DISTRIBUTION: Tropical Asia, Pakistan, India, Iran, and Australia.

West Pakistan: BALUCHISTAN: Shah Bilaweel, *Stocks s.n.* (K). Reported from Nasirabad, Rindli and Drabbi in Baluchistan.

2. **Ehretia** L. Syst. ed. 10. 936. 1759

Traxilum Raf. Sylva Telluriana 42. 1838.

TYPE SPECIES: *E. linifolia* L.

Trees or shrubs. Leaves small to large, usually distinctly petiolate, margins entire or serrate. Corolla white or yellowish, tube campanulate or elongate, lobes spreading or recurved; filaments elongate, anthers usually exserted; style terminal on the ovary, cleft above the middle, stigmas 2, small, capitate or elongate. Drupe subglobose, mostly yellow, orange or reddish, glabrous; endocarp at maturity breaking apart into either 2-seeded or 1-seeded pyrenes.

Species 50, all tropical, principally in the Old World, except 3 species in America.

KEY TO THE SPECIES

a. Leaves serrate. ..... 1. *E. serrata.*
a. Leaves entire.
  b. Leaves not exceeding 7.5 cm. in length, hairy beneath when mature; shrubby plants. ..... 2. *E. obtusifolia.*
  b. Leaves usually larger, reaching up to 12 cm. in length, glabrous beneath when mature; small trees. ..... 3. *E. laevis.*

1. **E. serrata** Roxb. (Hort. Bengal. 17. 1814, *nomen nudum*) Fl. Indica, ed. Carey & Wall. 2: 340. 1824, ed. Carey 1: 596. 1832; DC. Prodr. 9: 503. 1845, excluding vars.; Brandis, Forest Fl. India 339. 1874.

E. acuminata R. Br. var. *serrata* (Roxb.) I. M. Johnston, Jour. Arnold Arb. 32: 23. 1951.

TYPE: "in Bengalo orientali, Silhet etc." *Roxburgh s.n.* (CAL).

ICON.: Lindl. Bot. Reg. 13: *t. 1097.* 1827; Wight, Illustr. Indian Bot. 2: *t. 170.* 1841.

A medium-sized deciduous tree with rough not deeply fissured gray bark, twigs usually brownish-pubescent when quite young. Leaves 8–15(–20) cm. long, (3–)4–7(–10) cm. broad, usually lanceolate, sometimes elliptic-oblong, usually slenderly acuminate, margins finely and regularly serrate, the teeth ascending, usually with slender, prolonged, thickened, strict or incurved tips, base narrowed rarely rounded, midrib sparsely adpressed-hairy above, nerves slightly hairy in the axils beneath, otherwise glabrous; petioles 12–30 mm. long. Inflorescence of large terminal puberulous panicles with the lower branches axillary, 10–20 cm. long, 5–13 cm. broad. Flowers white, fragrant, sessile, 2.5 mm. across. Calyx sessile, 1.5–2 mm. long, lobes 0.8 mm. long, rounded, ciliate. Corolla 3–4 mm. long, nearly twice as long as the calyx, lobes 2–3 mm. long, about 1.5 mm. broad, blunt, spreading, tube about 1 mm. long. Filaments 2–3 mm. long. Style bifid, stigmas small, capitate. Drupe globose, nearly black when ripe, 3.5 mm. in diameter; pyrenes 2, each 2-celled, cells 1-seeded.

DISTRIBUTION: Assam to Kashmir and West Pakistan.

West Pakistan: HAZARA DIST.: Balakot, *Inayat 21993* (K); Haripur, *Kazmi 2474* (PES); Maksud near Haripur, 660 m., *R. R. Stewart 12561* (GH, K, RAW); Abbottabad, *Dickason s.n.* (MICH). RAWALPINDI DIST.: Rawalpindi-Murree Road, *R. R. Stewart 6120* (A). SWAT STATE: Saidu Sharif, *Kazmi 2464* (PES); Margzar, *R. R. Stewart 24306* (K, RAW), *Kazmi s.n.* (PES).

Kashmir: POONCH DIST.: Nawal Nadi, *R. R. Stewart s.n.* (K, RAW). Miscellaneous: Kashmir, *Falconer* Herb. East Ind. Co. *s.n.* (GH, K); Himal. Bor. Occid. *Thomson*, Hook. f. & Thoms. Herb. Ind. Orient. *s.n.* (GH, K). Reported from Jhelum Valley Road, Kishtwar, Udhampur and Jammu etc.

2. **E. obtusifolia** Hochst. ex DC. Prodr. 9: 507. 1845; C. B. Clarke in Hook. f. Fl. Brit. India 4: 142. 1883; Riedl in Rechinger, Fl. Iranica 48: 7. 1967.

E. obovata R. Br. in Salt. Voyage 64. 1814, *nomen nudum*; DC. Prodr. 9: 507. 1845, *in synon.*

TYPE: Abyssinia Distr. Medschara, *Schimper 2652* (B).

A deciduous shrub, young twigs clothed with brown pubescence and gray spreading hairs. Leaves 3–8 cm. long, 2–4 cm. broad, sometimes longer, variable in shape, usually obovate, rounded or retuse at the apices; covered thinly on both surfaces with usually scattered, sometimes dense, adpressed gray hairs, persistently hairy beneath; entire; petioles 5–18 mm. long. Inflorescence when young of close paniculate cymes, later lax and laterally corymbose, apparently terminal. Flowers pale bluish-white, 7–13 mm. across. Calyx 2.5 mm. long, externally hairy, lobes ovate-oblong, acute or subacute, ciliate. Corolla 6–8 mm. long, tube exceeding the

calyx, lobes about as long as the tube, blunt, spreading. Drupe globose to depressed globose 6 mm. in diameter; pyrenes usually 4.

DISTRIBUTION: Pakistan, Kashmir, India, and Abyssinia.

West Pakistan: ATTOCK DIST.: Campbellpur, Kala Chitta hills, 600 m., *R. R. Stewart 13620* (GH). GUJRAT DIST.: Pabbi hills, *R. N. Parker 3327* (A). HAZARA DIST.: Mirpur, *Kazmi 847* (PES). KOHAT DIST.: Thal, *Aitchison 515, 529* (GH). LAHORE DIST.: Changa Manga Forests, *Kazmi 2498* (PES). QUETTA DIST.: Harnai, *Lace s.n.* (K). RAWALPINDI DIST.: Murree Road, *R. R. Stewart 1671* (A); near Rawalpindi, *R. R. Stewart 13777* (GH). Miscellaneous: Shah Belaweel, *Stocks 539* (K). Reported from Salt Range, Kalat: Pab, Wahir and Las Bela, and Sind.

Kashmir: Kotli beyond Mirpur, *A. Rashid* in *R. R. Stewart 27243* (BM).

3. **E. laevis** Roxb. Coromandel Pl. 1: 42. *t. 56.* 1795, Fl. Indica ed. Carey & Wall. 2: 341. 1824, ed. Carey 1: 597, 1832; C. B. Clarke in Hook. f. Fl. Brit. India 4: 141. 1883; Brandis, Forest Fl. India 340. 1874, Indian Trees 481. 1921; Parker, Forest Fl. Punjab 362. 1924; Kashyap, Lahore Dist. Fl. 167. 1936; Riedl in Rechinger, Fl. Iranica 48: 7. 1967.

E. affinis Wall. Cat. No. 900. 1829, *nomen nudum.*
E. dichotoma Rottl. in Wall. Cat. No. 904. 1829.
E. punctata Roth, Nov. Pl. Sp. Indiae Orient. 126. 1821.
Beurreria laevis G. Don, Gen. Syst. 4: 390. 1838.
Beurreria punctata G. Don, Gen. Syst. 4: 390. 1838.
E. floribunda Benth. in Royle, Illustr. Bot. Himal. Mount. 1: 306. 1839.
E. laevis var. *floribunda* (Benth.) Brandis, Forest Fl. India 340. 1874; C. B. Clarke in Hook. f. Fl. Brit. India 4: 143. 1883.
E. laevis var. *platyphylla* Merrill, Lingnan Sci. Jour. 14: 55. 1935.

TYPE: "Circar Mountains" without citation of collector's name (CAL?).

ICON.: Roxb. l. c. *t. 56.* 1795; Wight, Icon. Pl. Indiae Orient. 4: *t. 1382.* 1848.

A small or large deciduous shrub to 10 m. tall tree, bark smooth gray, twigs glabrous or nearly so. Leaves ovate-elliptic or obovate or even suborbicular, 7–12 cm. long, 5–11 cm. broad, rounded or angled at bases and apices, when mature somewhat lustrous above, when young minutely glandular pubescent below, but except for some hairs in the vein axils becoming glabrous at maturity; petioles 1–2.5 cm. long. Inflorescence appearing just before leaf renewal, terminal and axillary, loosely dichotomous, with few bracts on the primary axis, otherwise naked, ultimate branches bearing sessile flowers unilaterally in two crowded ranks, hence somewhat scorpioid, particularly just before anthesis. Flowers white, sessile or subsessile. Calyx 1–2 mm. long, tawny-tomentose. Corolla 2.5–3.5 mm. long, subrotate, not conspicuous, tube open, 0.7–1.5 mm. long; lobes 2–2.5 mm. long, recurving. Style 2–3 mm. long, lobes as much as 1 mm. long. Drupe yellow or orange, 3–4 mm. diameter, endocarp rugose, breaking up at maturity into 4 single-seeded parts.

DISTRIBUTION: Iran, Pakistan, Kashmir, India, Burma, Hainan, Polynesia, Indochina, and Australia.

West Pakistan: ATTOCK DIST.: Kala Chitta hills, *R. R. Stewart 13608* (GH). HAZARA DIST.: Balakot, *Kazmi 2467* (PES). JHELUM DIST.: Mount. Tilla, *Kabir 20420* (RAW). LAHORE DIST.: Shahadra near Lahore, *R. R. Stewart 15375* (GH). PESHAWAR DIST.: near Peshawar, *R. R. Stewart 300b* (A). QUETTA DIST.: Torkhan Pass, above Harnai, *Kazmi 2488* (PES). Miscellaneous: Shah Bilaweel, *Stocks 607* (K).

Kashmir: Reported from Jhelum Valley, Mirpur, and Jammu.

3. **Coldenia** L. Sp. Pl. 125. 1753; Gen. Pl. ed. 5. 61. 1754.

TYPE SPECIES: *C. procumbens* L.

Usually branched, diffuse or prostrate herbs. Leaves small, crisped. Flowers white or yellow, sessile or nearly so. Calyx 4–5-partite, segments linear or lanceolate. Corolla tube short, rather broad, naked or with 4–5 appendages within, lobes 4–5, spreading, imbricate in bud. Stamens 4–5, inserted on the corolla tube, included; filaments short; anthers ovate. Ovary ovoid, slightly 4-lobed, 2-celled with 2 ovules or 4-celled with 1 ovule in each cell; styles 2, distinct, cohering from the base to the middle but easily separable, terminal; stigmas capitate. Drupe almost dry, of 4 subconnate, 1-seeded pyrenes. Seeds exalbuminous or with scanty albumen; cotyledons flat, broad; radical short, straight, incurved or incumbent on the cotyledons.

Species about 11, all American except the following, which is widely dispersed throughout the warmer regions.

C. procumbens L. Sp. Pl. 125. 1753; Aitch. Cat. Pl. Punjab & Sind 93. 1869; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 144. 1883; Cooke, Fl. Bombay Presidency **2**: 205. 1908.

TYPE: "Habitat in India" *Herb. No. 174. 1.* (LINN).

A procumbent herb, usually lying quite flat on the ground, stems reaching up to 45 cm. in length, shaggy with white hairs, branches often numerous, young parts silky with white hairs. Leaves crisped, 12–38 mm. long, 6–18 mm. broad, obovate-oblong, rounded at the apices, coarsely serrate or subpinnatifid, very hairy on both surfaces, base tapering; petioles shaggy, 3–9 mm. long. Flowers pale yellow, solitary, axillary, nearly sessile. Calyx divided to the base or nearly so, very hairy, segments 4, ovate, acute, ciliate, 2.5 mm. long. Corolla naked within, 2.5 mm. long. Stamens 4, scarcely higher than the corolla tube. Fruits dry 4-lobed pyramids, about 3 mm. long, 4 mm. broad at the widest part, grooved on two and ribbed on the other two sides, with a sharp central double beak, hairy, ultimately separating into 1-celled beaked pyrenes.

DISTRIBUTION: Pakistan, India, Ceylon, and tropics.

West Pakistan: Sind, *Stocks 549* (K).

4. **Heliotropium** L. Sp. Pl. 130. 1753; Gen. Pl. ed. 5. 63. 1754.

TYPE SPECIES: *H. europaeum* L.

Annual or perennial herbs or undershrubs, villous or scabrous. Leaves alternate. Spikes terminal, rarely axillary, dichotomous, branches short or long, scorpioid. Flowers usually white, light bluish, or rarely yellow, bracteate, ebracteate, or bracts much reduced. Calyx 5-partite or -lobed, segments lanceolate or linear, free, rarely coherent at the base. Corolla tubular, cylindrical or infundibuliform, usually hairy outside, sometimes also inside, lobes 5, plicate, subvalvate or imbricate, inflexed or patent, linear to roundish. Stamens 5, anthers sessile or with short filaments, inserted on the corolla tube, included, ovate to linear-lanceolate, rarely apiculate. Ovary completely or imperfectly 4-celled, 4-ovuled; style terminal, short or long, ending in a stigmatic disc, with a short or long, more or less conical appendage. Fruits dry, 2–4-lobed, of 4 or less nutlets. Seeds straight or curved, albumen small or none.

Species 275, in tropical and temperate zones of both hemispheres.

KEY TO THE SPECIES

a. Prostrate herbs; calyx divided up to 1/4 of its length, lobes short. Fruit enclosed by calyx. ..... 24. *H. supinum.*
a. Prostrate, decumbent or erect herbs or undershrubs; calyx divided nearly to the base, lobes free, long. Fruit not enclosed by the calyx.
  b. Plants completely glabrous. ..... 23. *H. curassavicum.*
  b. Plants variously hairy.
    c. Stigma with 2 linear, filiform, recurved arms, exserted from the corolla. ..... 7. *H. ophioglossum.*
    c. Stigma short, minutely lobed or not, always included in corolla.
      d. Inflorescence partly or fully bracteate, bracts sometimes much reduced.
        e. Stigma subcapitate, stigmatic ring fleshy and thick; corolla 1.5–2.5 mm. long, internally sparsely pilose from 0.5 mm. above the corolla base. ..... 1. *H. rarifolium.*
        e. Stigma elongate conic, stigmatic ring not fleshy, thin; corolla 2.5–4 mm. long, internally slightly or densely hairy only at the throat.
          f. Plants decumbent or prostrate; leaves lanceolate or elliptic; flowers sessile, closely set on the inflorescence. ..... 3. *H. marifolium.*
          f. Plants usually erect, sometimes decumbent; leaves linear to linear-lanceolate; flowers usually subsessile to pedicellate, rarely sessile; flowers distantly set on the inflorescence.
            g. Leaves linear, up to 45 mm. long, up to 3 mm. broad; inflorescence bracteate throughout. .. 4. *H. zeylanicum.*
            g. Leaves linear-lanceolate not exceeding 25 mm. in length, 3 mm. in width; lower flowers of the inflorescence evidently bracteate, in the upper flowers bracts much reduced or sometimes absent. ..... 2. *H. strigosum.*

d. Inflorescence ebracteate.
h. Corolla variously hairy within.
i. Corolla inside clearly with two hairy zones separated by a glabrous zone in between. ..... 17. *H. baluchistanicum.*
i. Corolla hairy inside, hairs neither in zones nor separated by any glabrous zone.
j. Corolla 2.5–3 mm. long; stigma sessile.
k. Inflorescence of closely set flowers; calyx lobes unequal; leaf bases obtuse to acute; anthers 0.5–0.6 mm. long; stigma 0.3–0.4 mm. long. ..... 22. *H. ovalifolium.*
k. Inflorescence of distantly set flowers; calyx lobes equal; leaf bases roundish or sometimes truncate; anthers 1 mm. long; stigma 0.9–1 mm. long. ..... 16. *H. remotiflorum.*
j. Corolla 4–8 mm. long; stigma subsessile or with style up to 0.7 mm. long.
l. Corolla 4–5 mm. long, lobes sublinear, plicate, inflexed into the corolla tube; stigma elongate-conical. ..... 11. *H. gillianum.*
l. Corolla 5–8 mm. long, lobes ovate or roundish, imbricate, patent; stigma compressed-conical.
m. Leaves lanceolate to ovate-lanceolate with short petioles, loosely covered with short, more or less erect hairs arising from tubercles, lower surface sometimes glabrous; flowers 3–7, loosely arranged; corolla uniformly hairy inside. ..... 14. *H. cabulicum.*
m. Leaves ovate to ovate-oblong with long petioles densely covered with long hairs apparently not arising from tubercles; flowers 7–20, closely arranged; corolla thickly hairy inside above the anthers and below the corolla lobes, and thinly so in between. ..... 18. *H. biannulatum.*
h. Corolla glabrous within.
n. Plants annual.
o. Plants grayish-white; inflorescence up to 12 cm. long with loose uniseriate flowers; calyx deciduous. ..... 19. *H. calcareum.*
o. Plants green to grayish-green; inflorescence 2–5(–8) cm. long with closely set biseriate flowers; calyx persistent.
p. Nutlets pubescent to often densely tomentose. ..... 20. *H. europaeum.*
p. Nutlets glabrous, slightly reticulate-rugose or indistinctly verruculose. ..... 21. *H. ellipticum.*
n. Plants perennial.
q. Corolla lobes broad, oblong, ovate or roundish, subvalvate or imbricate.
r. Leaves ovate, oblong-ovate or oblong-lanceolate; calyx 3.5–4 mm. long; corolla more or less 5 mm. long; nutlets free from the beginning. ..... 15. *H. ullophyllum.*

r. Leaves lanceolate to linear-lanceolate; calyx 1.75–2.5 mm. long; corolla 3–3.5 mm. long; nutlets 4, in 2 pairs or later free.
s. Nutlets not margined. ..... 6. *H. crispum.*
s. Nutlets margined. ..... 8. *H. bacciferum.*

q. Corolla lobes narrow, usually acute, plicate or subvalvate, inflexed in corolla tube when young, later more or less inflexed, suberect, or patent.
t. Leaves many times longer than broad, corolla lobes inflexed when young, later patent, caudate-acuminate. ..... 5. *H. subulatum.*
t. Leaves not much longer than broad; corolla lobes inflexed when young, later suberect or erect, not patent, not caudate-acuminate.
u. Anther connectives produced.
v. Leaves 15–25 mm. long, 15–20 mm. broad, ovate, orbicular or sometimes subcordate; corolla lobes 1 mm. long, linear. . 13. *H. aucheri.*
v. Leaves 3–12 mm. long and broad, ovate, rotund or truncate at base; corolla lobes 0.5 mm. long, narrowly triangular. ..... 12. *H. lamondiae.*
u. Anther connectives not produced.
w. Corolla 3–4 mm. long, lobes 0.7–1 mm. long, sinuses narrow, entire; anthers 1.2–1.5 mm. long, attached 1 mm. above the corolla base; style shorter than stigma. . 9. *H. dasycarpum.*
w. Corolla 4.5–5.5 mm. long, lobes 0.9–1.2 mm. long, sinuses broad, lobed or slightly dentate; anthers 1.2–2 mm. long, attached 1.8–2 mm. above the corolla base; style equalling the stigma. ..... 10. *H. brahuicum.*

1. **H. rariflorum** Stocks in Hook. Jour. Bot. **4**: 174. 1852; Boiss. Fl. Orient. **4**: 144. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 152. 1883; Cooke, Fl. Bombay Presidency **2**: 209. 1908; Burkill, Fl. Pl. Baluchistan 50. 1908; Riedl in Rechinger, Fl. Iranica **48**: 15. 1967.

TYPE: Baluchistan inferior (Karachi, Jemadar ka Landa), *Stocks 492* (K).

ICON.: Biol. Skr. 13(4): *fig. 150*. 1963.

Perennial undershrub, erect, 15–45 cm. tall. Stem and branches rigid, when young grayish-green, covered with short appressed hairs; brown when old, sometimes glabrous, bark peeling. Leaves linear-lanceolate, sessile, or short-petiolate, 20–35 mm. long, 3–5 mm. broad, subacute, entire, sometimes more or less revolute at margins, covered on both surfaces with short, stiff, appressed hairs. Inflorescence of slender, terminal and extra-axillary, bracteate spikes 2.5–7.5 cm. long; bracts sessile or subsessile 3–4 mm. long. Flowers white, sessile, distant. Calyx deeply 5-

lobed, lobes 1.5 mm. long, 0.6 mm. broad, lanceolate, obtuse to subacute, hairy externally and at the margins, more or less glabrous internally. Corolla 1.5–2(–2.5) mm. long, cylindrical-campanulate, externally hirsute, internally sparsely pilose from 0.5 mm. above the base, lobes 5, short, broadly ovate. Anthers 0.6 mm. long, ovate, inserted at or little above the middle of the corolla tube. Stigma depressed capitate, glabrous. Fruits 4-lobed, about 2.5 mm. across; nutlets 4, covered with appressed short hairs.

DISTRIBUTION: West Pakistan, Afghanistan, India, East and Southeast Africa.

West Pakistan: KALAT DIST.: Rar Kaur, southwest of Kalat, 1200 m., *Hotson 298* (GH). KARACHI DIST.: Karachi proper, Jemadar ka Landa, *Stocks 492* (K); Dumloti, *Tasnif* in *Kazmi 2459* (PES); North Nazimabad, Mangu-peer Road, *Jafri 3602* (E); Jangshahi, stony hillock, *Jafri 1576* (E). MAKRAN DIST.: Near Pasni, wind-blown sand deposits in foothills, *G. Popov 27a* (BM). THATTA DIST.: Thatta, *Bhola Puran* in *Cooke s.n.* (K).

2. **H. strigosum** Willd., Linn. Sp. Pl. **1**: 743. 1798; DC. Prodr. **9**: 546. 1845; Boiss. Fl. Orient. **4**: 143. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 151. 1883; Burkill, Fl. Pl. Baluchistan 50. 1908; Riedl in Rechinger, Fl. Iranica **48**: 15. 1967.

TYPE: "Habitat in Guinea" without citation of collector's name (B).

Perennial or rarely annual, prostrate, procumbent or erect, up to 30 cm. tall herbs. Stems tufted or intricately branched, covered with short, straight, stiff, appressed, white hairs. Leaves linear-lanceolate, 6–20(–25) mm. long, up to 2.5(–3) mm. broad, entire, subacute, sessile or the lower ones very short petiolate, clothed on both surfaces with short, stiff, white, appressed hairs up to 0.5 mm. long. Inflorescence 2.5–7.5 cm., in fruit to 15 cm. long, of solitary or geminate, bracteate spikes; bracts in the lower part up to 3 mm. long, above much reduced or, rarely, absent. Flowers white or pale blue with a tiny yellow eye; lower flowers pedicellate, pedicels 1–2 mm. long, upper subsessile to sessile. Calyx deeply 5-lobed, lobes up to 3 mm. long, lanceolate, cuneate, strigose externally. Corolla 3 mm. long, tubular or funnelform, strigose externally, the throat minutely and sparsely glandular and puberulent at the summit internally, lobes oblong or very short and broad, somewhat involute in bud. Anthers 0.75 mm. long, ovate-lanceolate, tips thickened and coherent when young; filaments 0.5 mm. long, inserted 0.5 mm. above the corolla base. Style distinct, 0.4 mm. long; stigma 0.5 mm. long, with a distinct stigmatic ring about 0.3 mm. in diameter and superimposed on a narrowly conic sterile appendage. Fruits rounded or lobed, depressed or globose, covered with closely set, appressed hairs; nutlets 4, about 1 mm. high.

DISTRIBUTION OF SPECIES: Africa, Arabia, Afghanistan, Pakistan, Kashmir, India, Ceylon, Burma, Siam, Hainan, Fukian, Macao, and Hongkong.

2a. Subsp. **strigosum.**

Usually procumbent to erect; stems tufted; stem, branches and leaves covered with closely set trichomes giving the whole plant a grayish-white aspect. Leaves 15–20(–25) mm. long. Fruits 4-lobed, depressed at the top towards the style.

DISTRIBUTION OF SUBSP.: Africa, Arabia, West Pakistan, India, and Ceylon, probably introduced in Australia.

West Pakistan: ATTOCK DIST.: Between Hazro and Saidan, ca. 2 miles north of Grand Trunk Rd., dry sandy roadsides, *Burtt 686* (E). BANNU DIST.: In collibus arenosis Pezu, inter Dera Ismail Khan et Bannu, 400 m. *Rechinger 30035* (G, W). DADU DIST.: Karachi to Dadu, ca. 10–15 km. south of Sehwan, outermost limestone outcrop, *Lamond 846* (E, G); *Rechinger 28718* (G, W). DERA ISMAIL KHAN DIST.: Sulaiman Range, Fort Sandeman to D. I. Khan, ca. 100 km. from Fort Sandeman, between Mughal Kot and Daraban, conglomerate slopes, 700–900 m. *Kazmi 1970* (PES); *Lamond 1505* (E); *Rechinger 29977* (G, W). HYDERABAD DIST.: Tandojam, Bholari Camp, *M. Ahmad 49* (MICH). JHELUM DIST.: Balkasar oil fields on Chakwal-Balkasar Road, *Arif J. Ahmad s.n.* (PES); Rawalpindi to Jhelum, east of Sohawa, rocky hillsides, *Burtt 1149* (E); Salt Range above Mandiala, *Fleming 73* (E). KOHAT DIST.: Between Gumbat and Khushalgarh, near junction of roads from Attock bridge, *Burtt 1090* (E). MAKRAN DIST.: Bela, Hab to Diwana, ca. 10 km. from Hab, weed of *Ricinus* fields, *Lamond 772* (E); Bela, 14 km. west of Bela, road to Turbat, sandy plains near foothills, 80 km. *Lamond 291* (E). QUETTA DIST.: Mach, 1000 m. *Jafri 2803* (E); Chuper Rift, 1600 m. *Lace s.n.* (E). RAWALPINDI DIST.: Rawalpindi, Sau (?) hills, *Aitchison 471* (K); Rawalpindi, 570 m. *Kazmi s.n.* (PES), *R. R. Stewart 949* (GH).

2b. Subsp. **brevifolium** (Wall.) Kazmi, comb. nov.

H. brevifolium Wall. in Roxb. Fl. Indica ed. Carey & Wall. **2:** 2. 1824; DC. Prodr. **9:** 546. 1845; Riedl in Rechinger, Fl. Iranica **48:** 16. 1967.
H. strigosum Willd. var. *brevifolium* (Wall.) C. B. Clarke in Hook. f. Fl Brit. India **4:** 151. 1883.

TYPE: India, *Wallich 914* (K).

Decumbent, prostrate or erect, intricately branched; stem, branches, and leaves covered with loosely set trichomes giving the whole plant a greenish-white appearance. Leaves up to 15 mm. long. Fruits not or slightly lobed, not depressed at the top, plane or slightly produced towards the style.

DISTRIBUTION OF SUBSP.: Afghanistan, Pakistan, Kashmir, India, Nepal, Burma, Siam, Hongkong, Hainan, Fukian, and Macao.

West Pakistan: DERA ISMAIL KHAN DIST.: Dera Ismail Khan Proper, banks of Indus, 240 m. *Deane 23* (K). HAZARA DIST.: Balakot, *Jafri & Ali 3262* (E); Mansehra, *Kazmi s.n.* (PES). KARACHI DIST.: Karachi to Mugar Peer, *Perry s.n.* (K); near Behar Colony, along Lyari river, *Jafri 860* (E); in agris incultis, 10–20 km. n. Hab Chauki, *Rechinger 28618* (G, W); Dabbiji, *Koelz 7604* (MICH). LAHORE DIST.: Lahore Proper, *N. (Nath ?) s.n.* (E). LYALLPUR DIST.: Lyallpur proper, *R. R. Stewart s.n.* (18. 3. 1917) (K). PESHAWAR DIST.: Peshawar to

Jhelum, *J. L. Stewart 271/P* (GH). RAWALPINDI DIST.: Rawalpindi Proper, 570 m. *R. R. Stewart 9494A* (GH); Topi Park, *R. R. Stewart 7521* (K); Sangla Hill desert, *R. R. Stewart 1376* (K); between Rawalpindi and Jhelum, stony hillside, *Burtt 620* (E); Panjar, *R. R. Stewart 2853* (E); *Kazmi 2485* (PES); Dhamyal, 560 m. *Nath* in *R. R. Stewart 17259a* (GH).

Kashmir: MUZZAFFARABAD DIST.: Lower Kishanganga Valley, near Muzzaffarabad, *R. R. Stewart 17317* (GH). JAMMU DIST.: 10 miles from Jammu, 470 m. *R. R. Stewart 12595* (GH).

The subspecies *strigosum* and *brevifolium* are similar in details of the form of leaves and structure of flowers. Subspecies *brevifolium* differs in habit from the former in usually being decumbent, sometimes prostrate, or at times even erect. The whole plant is less hairy in comparison to subsp. *strigosum*, the trichomes are loosely set and the leaves are shorter. The fruits are plane at the top or more or less produced towards the style. Subspecies *strigosum* has a westerly distribution, while subsp. *brevifolium* represents the eastern range of distribution of the species. West Pakistan and some Western and Central parts of India are actually the areas where these two subspecies overlap and, therefore, in these areas many intermediate forms are found.

3. **H. marifolium** Retz. Obs. Bot. 2: 8. 1781; DC. Prodr. 9: 547. 1845; C. B. Clarke in Hook. f. Fl. Brit. India 4: 152. 1883; Cooke, Fl. Bombay Presidency 2: 213. 1908, excluding syn. *H. rottleri* Lehm.

TYPE: Not indicated. (Described from Koenig's collection from South India.)

Perennial, decumbent or prostrate herb; stems up to 15 cm. long; branches usually spreading near the root, clothed densely or loosely with stiff appressed hairs; hairs 0.5–1 mm. long. Leaves lanceolate to elliptic, 8–20 mm. long, 2–5 mm. broad, earliest ones alternate, fascicled or subopposite, the later ones all alternate, midrib impressed above and prominent beneath, margins usually slightly revolute, apices acute or subacute, bases obtuse or acute, sessile or petiolate; petioles up to 2 mm. long; leaves covered on both surfaces with stiff, straight trichomes, sometimes arising from minute tubercles, trichomes usually more dense below. Inflorescence at first glomerate, in fruit a crowded or loose biseriate scorpioid cyme, 1–3(–4) cm. long; bracts spreading, foliaceous, lanceolate, 1–4 mm. broad. Calyx 2–4 mm. long, divided to the base, lobes appressed hispid, lanceolate, becoming enlarged ovate-lanceolate in fruit, calyx sessile or very short pedicellate in fruit. Corolla white, 2.5–3.5 mm. long, not much surpassing the calyx, hairy externally, lobes short, broad, erect, or infolding in bud, throat at summit slightly or densely minutely villose. Anthers 0.7 mm. long, lanceolate; filaments 0.2 mm. long, inserted 0.5–0.7 mm. above the corolla base. Ovary glabrous; stigma 0.5 mm. long, stigmatic disk 0.3 mm. in diameter; style 0.2–0.3 mm. long. Fruits depressed, rounded or lobed, covered partly or fully with short thick hairs, sometimes glabrous.

DISTRIBUTION OF SPECIES: Pakistan, India, and Ceylon.

3a. Subsp. **marifolium.**

Decumbent or prostrate, much branched; branches up to 15 cm. long. Leaves broad lanceolate, acute, 18–20 mm. long, 2–5 mm. broad, short petiolate, covered thinly with sharp trichomes usually arising from tubercles; petioles up to 2 mm. long. Bracts 3–4 mm. long, broadly lanceolate, leaf-like. Corolla throat densely hairy. Fruits bearing trichomes on the top, or glabrous.

DISTRIBUTION OF SUBSP.: South India and Ceylon.

3b. Subsp. **wallichii** (C. B. Clarke) Kazmi, comb. nov.

H. marifolium var. *wallichii* C. B. Clarke in Hook. f. Fl. Brit. India **4**: 152. 1883.

TYPE: India, *Wallich 2092* (K).

Usually prostrate rarely decumbent, much branched; branches up to 10 cm. long. Leaves lanceolate, subacute, usually sessile or sometimes the middle leaves very shortly petiolate, 4–10 mm. long, 1.5–2.5 mm. broad, densely covered on both surfaces with stout, white trichomes not usually arising from tubercles, 0.5–1 mm. long; petioles 0.5 mm. long. Bracts lanceolate, 1–2 mm. long, to 1 mm. broad. Corolla throat less hairy. Fruits densely and totally covered with short stout trichomes. Spikes longer than those of subsp. *marifolium*, up to 4 cm. long.

DISTRIBUTION OF SUBSP.: Central and southern parts of West Pakistan, and Rajputana in India.

West Pakistan: BANNU DIST.: Tutaki, 50 km. north of Bannu, 700 m. *Rechinger 30093* (G, W). DADU DIST.: Amri near Sehwan, near Railway Station, *Jafri 2756* (E). KARACHI DIST.: Drigh Road near Dalmia Cement Factory, *Baquar* in *Kazmi 2460* (PES); 12 km. west of Bela, *Rechinger 27583* (G, W); Inter Damloti et Khadiji, *Rechinger 28502* (G, W).

I did not see the type of C. B. Clarke's variety *wallichii* but the other collections in Herb. Ind. Or. Hook. f. & Thoms., determined by Clarke, agree with the specimens cited above from West Pakistan. Subspecies *wallichii* is evidently distinguishable from subsp. *marifolium* by having much shorter and narrower leaves and bracts and longer spikes. The leaves are thickly covered with stouter and longer hairs, usually not arising from tubercles. The plants are mostly prostrate. Subspecies *wallichii* represents the northern area of distribution of *H. marifolium*.

4. **H. zeylanicum** (Burm. f.) Lam. Encycl. Méth. Bot. **3**: 94. 1791.

H. curassavicum L. var. *zeylanicum* Burm. f. Fl. Indica 41. *t. 16, fig. 2*. 1768. *H. linifolium* Lehm. Asperif. 35. 1818; DC. Prodr. **9**: 547. 1845.

TYPE: South India: Tuticorin, *Garcin* (G).

Usually annual or sometimes perennial, erect, up to 40(–55) cm. tall,

usually branched near the base, branches long and straight; stem and branches pale green to pale brown, or brown at maturity, loosely covered with short appressed trichomes, up to 0.6 mm. long, arising from tuberculate bases, sometimes the lower stem quite glabrous. Leaves subsessile or the lower ones short petiolate, linear, acute, entire, usually revolute at margins, up to 7 cm. long and 3 cm. broad, upper surface slightly hairy or rarely glabrous, lower surface loosely hairy with appressed trichomes, sometimes minutely tuberculate at the base and up to 5 mm. long. Inflorescence terminal or axillary, simple or forked, 3–5 cm. long, in fruit becoming elongated to 10 cm., bearing uniseriate, bracteate flowers or fruits; bracts 2(–3) mm. long, linear, hairy. Calyx sessile or subsessile, or with pedicels hardly up to 0.5 mm. long, divided to the base, lobes lanceolate, more or less acute, hairy outside, usually more on the lower half and at margins, glabrous inside, sometimes subequal, 1.5–2.5 mm. long, 0.5–1 mm. broad. Corolla white with a tiny yellow eye, sparsely hairy externally and slightly so at the throat within, 3.5–4 mm. long, tube 1.5–1.7 mm. long, slightly swollen in the middle, narrowed at mouth, lobes plicate, patent or fully expanded, ovate, rounded or slightly obtuse at the tips, with prominent veins, 1.4–1.6 mm. long, 1–1.2 mm. broad. Anthers ovate, acutish, 0.8 mm. long; filaments about 0.2 mm. long, inserted 0.7 mm. above the corolla base. Ovary glabrous, style very short, 0.1 mm. long, stigma conical, 0.5 mm. long, stigmatic ring conspicuous. Fruits compressed, lobed, covered with loose short trichomes; 2.5 mm. diameter, 1.5 mm. high.

DISTRIBUTION OF SPECIES: Pakistan, India, Ceylon, Siam, Australia, and East Africa.

4a. Subsp. **zeylanicum.**

Calyx up to 1.5 mm. long; corolla 3.5 mm. long, corolla tube much exceeding the calyx; leaves comparatively narrower than those of subsp. *paniculatum*.

DISTRIBUTION OF SUBSP.: South India and Ceylon.

4b. Subsp. **paniculatum** (R. Br.) Kazmi, comb. nov.

H. paniculatum R. Br. Prodr. 494. 1810; DC. Prodr. **9**: 547. 1845; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 151. 1883; Cooke, Fl. Bombay Presidency **2**: 212. 1908.

TYPE: "Habitat in Novae Hollandiae littore intra tropicum" without citation of collector's name (BM, G-DC).

Calyx 2.5 mm. long; corolla 3.5–4 mm. long, corolla tube more or less equalling the calyx, more hairy outside; leaves comparatively broader than those of subsp. *zeylanicum*.

DISTRIBUTION: East Africa, Pakistan, India, Siam, and Australia.

West Pakistan: HAZARA DIST.: Khanpur, *R. R. Stewart 28893* (E). JHELUM

DIST.: Rawalpindi to Jhelum, East of Sohawa, rocky hillsides, fl. white with yellow eye, *Burtt 1150* (E). MARDAN DIST.: 15 miles northeast of Mardan, just south of Machai, on open places and rocky hillsides dominated by *Acacia modesta*, fl. white with yellow eye, *Burtt 1518* (E). RAWALPINDI DIST.: Rawalpindi, Topi Park, *R. R. Stewart 7520* (K). SHAHPUR DIST.: Sakesar, *Drummond 14560* (E). Miscellaneous: Sind ?, *Stocks s.n.* (K).

Heliotropium zeylanicum (Burm. f.) Lam. is based on *H. curassavicum* var. *zeylanicum* Burm. f., which was collected in Tuticorin, South India, by Garcin. It was the figure by Burmann (l. c. *t. 16, fig. 2*) from which Lamarck took his description. Wight (Illustr. Indian Bot. 2: *t. 170b.* 1841) referred it to his *Tournefortia zeylanica*, and later treated it as *Heliotropium zeylanicum* (Icones Pl. Indiae Orient. 3: *t. 892.* 1849). C. B. Clarke (in Hook. f. Fl. Brit. India 4: 148. 1883) adopted the name *H. zeylanicum* (Burm. f.) Lam. for the plant figured by Wight and this was carried on later by many authors.

As pointed out by Trimen (Fl. Ceylon 3: 199. 1895), proposed by Cooke (Fl. Bombay Presidency 2: 208. 1908), and concurred in by Duthie (Fl. Gangetic Plain 2: 92. 1911), the plant figured by Burmann is different from the plant drawn by Wight. Actually Wight's figure represents *Heliotropium subulatum* (DC.) Vatke, described from the type collected by Schimper in Abyssinia, and has the characteristic caudate-acuminate corolla lobes.

Burmann's figure, in all its details, strictly represents the plant which was later described by Lehmann as *Heliotropium linifolium* from South India or Ceylon.

Subspecies *zeylanicum* agrees in all its characters with subsp. *paniculatum*, except that the calyx in the former is only up to 1.5 mm. long and the corolla tube much exceeds the calyx in length, while in the latter the calyx is more or less equal to the corolla tube. The typical subspecies is confined to South India and Ceylon, while subspecies *paniculatum* is widely distributed.

5. **H. subulatum** (DC.) Vatke, Oesterr. Bot. Zeitschr. **25**: 166. 1875.

Tournefortia subulata Hochst. ex DC. Prodr. **9**: 528. 1845.
T. edgeworthii DC. Prodr. **9**: 527. 1845.
T. royleana DC. Prodr. **9**: 527. 1845.
Messerschmidia hispida Benth. in Royle Illustr. Bot. Himal. Mount. **1**: 306. 1839.

TYPE: Abyssinia, *Schimper 1285* (B).

ICON.: Wight, Icones Pl. Indiae Orient. 3: *t. 892.* 1849, under *H. zeylanicum*.

A perennial, but flowering in the first year, erect, to 60 cm. tall. Stem and branches covered with spreading trichomes arising from tuberculate bases. Leaves lanceolate, usually narrowed at both ends, lower short petiolate, upper subsessile, acute, margins entirely or slightly undulate, covered on both surfaces with short subappressed trichomes mixed with

long spreading ones arising from minute tuberculate bases, nerves sunken on the upper surface, raised and prominent below, (8–)10–50(–60) mm. long, (2–)4–8(–15) mm. broad. Inflorescence 5–15 cm. long, terminal or axillary, slender, simple or forked, bearing closely set uniseriate flowers or distant fruits, ebracteate. Calyx sessile, deeply 5-lobed, lobes lanceolate, with few short appressed hairs externally, and more densely hairy on the margins, marginal hairs 1.5 mm. long. Corolla white to dirty yellow, 3.5–5 mm. long, with minute appressed trichomes, sometimes arranged in rows outside, glabrous within, corolla tube cylindrical, swollen in the upper part, contracted at throat, lobes incurved in young flowers later patent, caudate acuminate, 1–1.5 mm. long. Anthers oblong, slightly exserted, 1 mm. long, filaments very short, inserted about 2 mm. above the corolla base. Stigma conical, hispid, shorter than the glabrous style. Fruits 2 mm. diameter; nutlets 4, separating first in pairs, later free, brown, rugose or pitted.

DISTRIBUTION: Northeast and central Africa, West Pakistan, and India.

West Pakistan: JHELUM DIST.: Salt Range, sandstone hills above Mandiala, *Fleming 68* (E). KARACHI DIST.: Karachi near Nazimabad, along dry border of Lyari river, fl. dirty yellowish, *Jafri 817* (E); Karachi University Campus, *Rechinger 27533* (G, W), *27534* (W), *Abid 37*, *Kazmi s.n.* (PES); Drigh Road, *Jafri s.n.* (E).

Tournefortia zeylanica Wight (Illustr. Indian Bot. 2: *t. 170b.* 1841) is a misidentification.

6. **H. crispum** Desf. Fl. Atlant. 1: 151. *t. 41.* 1798.

Lithospermum hispidum Forssk. Fl. Aegypt.-Arab. 39. 1775.
H. undulatum Vahl var. *ramosissimum* Lehm. Asperif. 24. *t. 40.* 1831.
H. ramosissimum (Lehm.) DC. Prodr. **9:** 536. 1845; Riedl in Rechinger, Fl. Iranica **48:** 18. 1967.
H. nubicum Bunge, Bull. Soc. Nat. Moscou **42**(2): 330. 1869.
H. persicum Boiss. Fl. Orient. **4:** 147. 1875, *non* Lehm.
H. afghanum Boiss. *Ibid.* 143. 1875.
H. turcomanicum M. Pop. & Korov. Acta Horti Petrop. **42:** 246. 1931.
H. sarothroclados Bornm. Beih. Bot. Centralbl. **61**(B): 89. 1941.

TYPE: "Habitat in arenis prope Tozzer et Elhammah" without citation of collector's name (P).

ICON.: Desf. Fl. Atlant. *t. 41.* 1798.

Perennial, usually erect (sometimes suberect or rarely prostrate herb), sometimes shrubby with woody base to 1 cm. thick, up to 60 cm. tall, branched; stem and branches grayish-green, covered with short stiff trichomes mixed with scattered stouter ones arising from tuberculate bases. Leaves lanceolate to linear-lanceolate, lower cauline leaves subsessile or short petiolate, upper cauline leaves usually sessile, sometimes subsessile, margins crenulate, undulate or subentire, nerves and veins sunken on the upper surface, prominent below, covered on both surfaces

with stiff white hairs, intermixed with thicker hairs arising from tuberculate bases, 30–40 mm. long, 5–7.5 mm. broad. Inflorescence terminal, sometimes axillary, usually bifurcate or sometimes solitary, short when young, later much elongated, 2–7 cm. long, bearing single-ranked, ebracteate, usually distant flowers. Calyx sessile, persistent, divided to the base, thickly hairy outside, inside almost glabrous, 1.75–2.5 mm. long, lobes lanceolate, acute. Corolla white, 3–3.5 mm. long, exceeding the calyx, tubular, hairy outside, glabrous within; lobes imbricate, oblong-ovate or roundish with crenulate margins, 0.7–0.9 mm. long. Anthers sessile, 0.8–1 mm. long, inserted 1 mm. above the corolla base. Stigma conic-elongate, slightly furrowed, minutely bifid at the apex, 0.8 mm. long; style inconspicuous. Fruits lobed, covered with long or short hairs, surface slightly rugulose, 2.5 mm. high, 2.25 mm. in diameter; nutlets 4, not margined, when young in pairs, later free.

DISTRIBUTION: Senegal, Tunis, Egypt, Sinai, Transjordan, Iraq, Aden, South Arabia, Iran, Afghanistan, West Pakistan, and India.

West Pakistan: ATTOCK DIST.: Campbellpur, *R. R. Stewart 7756* (KAU, MICH), *15308* (GH), *448* (KAU), *Vergury s.n.* (BM). CHAGAI DIST.: E. of Nokundi, sandy roadside, *Lamond 136* (E); 100–150 km. E. Nokundi, in deserto, *Rechinger 27271* (G, W). DADU DIST.: Karachi to Dadu, ca. 10–15 km. S. of Sehwan, outermost limestone outcrop, *Kazmi 1366b* (PES); *Lamond 870* (E, G); *Rechinger 28719* (G, W). DERA ISMAIL KHAN DIST.: Tank, *Duthie 7173* (E, K). JHELUM DIST.: Salt Range, *Fleming 69* (E); Langerpur, *R. R. Stewart 524* (MICH), *526* (K), *445* (KAU); Bhaun, *Bhal 447* (KAU); Khewra, *Iftakhar* Herb. No. 7302 (LAH). KALAT DIST.: ca. 20 km. W. of Bela, W. of Jan Pass, rocky plateau, 300 m., *Lamond 310* (E); 30 km. W. of Bela, *Lamond 316* (E, G); Khuzdar to Wad, ca. 30 km. from Khuzdar, 1150 m. *Lamond 205* (E); 10 km. S. Khuzdar, *Rechinger 27392* (G, W). KARACHI DIST.: Karachi Proper, Housing Society, *Ruqayya Islam s.n.* (KAU); *Kazmi s.n.* (PES); Off Malir Cantt., Momen Gate, *Jafri 1276* (E); Bela, between Hab River and Uthal, *Lamond 266* (E, G), *270* (E); Malir riverside, *Tasnif* in *Kazmi 2461* (PES); Hawkes Bay, *Ali s.n.* (KAU); Dabbiji, *Koelz 7600* (GH, MICH). KHYBER AGENCY: Torkham, *Anwar 78* (PEU); near Jamrud, *Kazmi s.n.* (PES); Landi Kotal, *Kazmi s.n.* (PES). LAHORE DIST.: Lahore, *Williams s.n.* (E); *J. L. Stewart 2582* (K); Mugla near Lahore, *Herb. Ind. Or. Hook. f. & Thoms. s.n.* (K). MAKRAN DIST.: Between Hoshab and Punjgur, ca. 20–30 km. from Punjgur, sandy plains, *Kazmi 1158* (PES); *Lamond 578* (E); near Punjgur, 900 m., *Popov 164, 188* (BM). MIANWALI DIST.: Mianwali, *Kazmi 1148* (PES); Kalabagh, *Kazmi s.n.* (PES); *Bamber s.n.* (LAH); Mirjal, *A. Ali s.n.* (PFI–M). MUZZAFFARGARH DIST.: Thal, *Sadiq Masih s.n.* (KAU). PESHAWAR DIST.: near Akora, ca. 4 miles W. of Attock Bridge, fl. white, *Burtt 557* (E); Peshawar, *Deane s.n.* (K); *Nath* in *R. R. Stewart 15465* (GH); *J. L. Stewart 115/P* (GH); Tehkal, *Hashim 11* (PEU); Amangarh, *S. R. Khan s.n.* (PEU); Peshawar Cantt., *Kazmi s.n.* (PES). QUETTA DIST.: Quetta, *Lace 3420* (E); in Valle 12 km. N. Murgha Kibzai, Substr. Tonscheifer, 1600 m. *Rechinger 29806* (G, W). RAWALPINDI DIST.: Rawalpindi, *Aitchison 472* (K); *R. R. Stewart 13792* (GH); *Kazmi 2462* (PES); Margalla near Rawalpindi, 650 m. *R. R. Stewart 14664a* (MICH); *14664* (GH); Margalla towards Taxila, *Nath* in *R. R. Stewart 1166* (KAU); Taxila, *Nasreen Zahida 31* (PEU); *K. L. Basin s.n.* (ICP). WAZIRISTAN AGENCY: Dattkhel, *Qizilbash 102* (ICP). ZHOB DISTR.:

Fort Sandeman, *Dick-Peddie 304* (KAU). Miscellaneous: Punjab. *Herb. Ind. Or. Hook. f. & Thoms. s.n.* (BM, GH, MICH).

Heliotropium crispum is very variable in the size and pubescence of its leaves. The four nutlets in the unripe fruits remain coherent in pairs and are separated later at ripening of the fruits. The important characters which distinguish this species from its allies are its usually longer inflorescence bearing lax flowers with corollas quite exceeding the calyx; its fruits not at all depressed at the top, but produced towards very short or inconspicuous styles; and its nutlets unwinged at the margins.

7. **H. ophioglossum** Boiss. Fl. Orient. **4**: 145. 1875.

H. ophioglossum Stocks ex Aitch. Cat. Pl. Punjab & Sind 94. 1869, *nomen nudum*; C. B. Clarke in Hook. f. Fl. Brit. Ind. **4**: 149. 1883; Cooke, Fl. Bombay Presidency **2**: 208. 1908; Riedl in Rechinger, Fl. Iranica **48**: 17. 1967.

H. ditrichum Stocks *in exsicc.*

TYPE: "Sind: Jemidar ka Landa near Kurrachi" *Stocks 466* (as *H. Ditricho*) (K).

Perennial shrub, erect, 15–50 cm. tall, branched from near the base. Stem and branches clothed with soft trichomes intermixed with stiff long ones (up to 2.5 mm. long) arising from white tuberculate bases. Leaves lanceolate, elliptic or rarely oblanceolate, margins subentire or slightly undulate, apices acute, 1–4(–5) cm. long, 6–12 mm. broad, lower subsessile to very short petiolate, upper usually sessile or subsessile, covered on both surfaces with soft short trichomes intermixed more or less uniformly on the upper surface and mostly on the raised midrib and veins of the lower surface, with stout trichomes up to 2.5 mm. long arising from white tuberculate bases. Inflorescences terminal, simple, geminate, or ternate, densely hairy, 5–15 cm. long, bearing 1–2-ranked, sessile (on the lower part distant) flowers. Calyx falling with the fruit, divided almost to the base, lobes linear-lanceolate, acute, covered externally with long stiff trichomes, internally with comparatively thinner ones, 3–4 mm. long, 0.5–1 mm. broad. Corolla white, slightly exceeding the calyx, cylindric, minutely scabrous externally, glabrous inside, lobes broadly oblong-ovate or suborbicular, obtuse to subacute, undulate, veined, usually with small intermediate teeth in the sinuses, 1 mm. long. Anthers linear-oblong, at tips obtuse, sessile, inserted below the middle of the corolla tube, 2 mm. long. Style very short, stigma short conical at base, prolonged above into a long subulate appendage about 4 mm. long, divided from the apex, for about 1/3 its length, into two filiform recurved acute arms, which are exserted beyond the corolla. Fruits 1.5 mm. long, slightly lobed, dark brown to blackish; nutlets 4, rounded on the back, with mealy apex.

DISTRIBUTION: West Pakistan.

West Pakistan: DADU DIST.: Karachi to Dadu, Thano Bula Khan to Kotri,

outermost limestone ranges, *Lamond 820* (E). KARACHI DIST.: Karachi, Jemidar ka Kanda, *Stocks 466* (K); in *Herb. Ind. Or. Hook. f. & Thoms. s.n.* (BM, GH); Karachi University Campus, *Meher Jahan s.n.* (KAU); *Nusrat Farida s.n.* (KAU); *Kazmi s.n.* (PES); Mungo Pir, *Rehman* in *R. R. Stewart 25722* (KAU); Manora and Mungo Pir, *Salim 25* (BM); Kinghar Lake (Kinghar Dhan), *Koelz 7599* (MICH); Dabbiji, 35 miles E. of Karachi, grayish woody, 1 ft. high with white flowers, bare ground on roadside, *Burtt 1567* (E); north Nazamabad, stony hill base, *Jafri 3733* (E); Drigh Road, sandy ground, *Jafri 917* (E); Maripur, *Stearn 12* (K); Malir Cantt., *Abid 35* (PES); Bela to Diwana, ca. 10 km. from Hab, weed of *Ricinus* fields, *Lamond 373* (E); *Kazmi 903b* (PES); 10–20 km. N. Hab Chowki, in cultis, *Rechinger 28617* (G, W). Miscellaneous: Sind, *Dalzell 16* (K); *Bhola s.n.* (E).

8. **H. bacciferum** Forssk. Fl. Aegypt.-Arab. 38. 1775.

TYPE: Arabia Felix: Lohaja *Forsskål* (C).

Perennial, usually erect, sometimes decumbent or procumbent herb or shrub, usually with woody base, sometimes deeply grooved and up to 3 cm. thick; stem much branched, primary branches usually long, the secondary short, more or less divaricate, covered with appressed or erect, thin or thick, short trichomes, usually arising from white tuberculate bases. Leaves very variable, short, terete, sessile to long, broad, flat, subsessile or tapering at both ends, short petiolate, 10–60 mm. long, 1–10 mm. broad, margins crenulate, undulate and usually revolute, nerves sunken or inconspicuous on the upper surface, prominent and raised on the lower surface, acute, covered on both surfaces with variable, short or long, thin or thick trichomes, from white tuberculate bases or not. Inflorescence strongly reduced, hardly up to 2.5 cm. long, usually with short naked peduncles, mostly in pairs, bearing few, closely set, sessile, ebracteate flowers. Calyx persistent, divided nearly to the base, covered densely with trichomes, lobes ovate-lanceolate, acute. Corolla white, 2.5–3 mm. long, cylindrical, densely covered with trichomes on the outside, glabrous within, corolla tube slightly narrowed at the throat, more or less equalling the calyx, lobes imbricate, very short, hardly 0.6–0.7 mm. long, ovate, sometimes truncate, rarely with short-lacerate margins. Anthers subsessile, oblong, inserted at or below the middle of the corolla tube, 1–1.25 mm. long. Style up to 0.75 mm. long; stigma 1 mm. long, conical, short bifid at the apex, slightly hairy with inconspicuous stigmatic ring. Fruits globose, 2 mm. long and broad; nutlets 4, in 2 pairs, ± winged, smooth, rugulose, or warty, glabrous or sometimes ± hairy.

DISTRIBUTION OF SPECIES: Senegal, Morocco, Tunis, Algeria, Libya, Egypt, Arabia, Iran, and West Pakistan.

KEY TO THE SUBSPECIES AND VARIETIES

a. Marginal wings of nutlets broad; line of separation of the 2 nutlets in a pair not conspicuous. ..... 8a. subsp. *bacciferum*.
b. Leaves usually flat, 5–7 mm. broad. ..... 8aa. var. *bacciferum*.
b. Leaves usually terete, 2–3 mm. broad. ..... 8ab. var. *tuberculosum*.

a. Marginal wings of nutlets narrow; line of separation of the 2 nutlets in a pair conspicuous. ..... 8b. subsp. *lignosum*.
c. Leaves usually short and terete, sometimes flat; line of separation of the 2 nutlets in a pair deep. ..... 8ba. var. *lignosum*.
c. Leaves never terete, always flat, lanceolate; line of separation of the 2 nutlets in a pair not as deep as in var. *lignosum*. ... 8bb. var. *fartakense*.

8a. Subsp. **bacciferum**.

Nutlets always joined in pairs, pairs winged at the separating margins; wings conspicuous and broad; in every pair of nutlets the line of separation of two nutlets is not conspicuous.

DISTRIBUTION OF SUBSP.: As for the species.

8aa. Var. **bacciferum**.

Leaves usually flat, up to 35 mm. long, 5–7 mm. broad, covered on both surfaces with trichomes not arising from tuberculate bases, or sometimes intermixed with the trichomes arising from tuberculate bases, but only in older leaves.

West Pakistan: DADU DIST.: In collibus calc., 10–15 km. S. Sehwan, *Rechinger 28739* (G, W); *Bhola Puran 6* (K). DERA ISMAIL KHAN DIST.: In arenosis montibus, 50 km. N. Dera Ismail Khan, 250 m. *Rechinger 30025* (G, W). HYDERABAD DIST.: Hyderabad, *Cook s.n.* (K). KALAT DIST.: 30–35 km. W. Bela, *Rechinger 27670* (G, W). KARACHI DIST.: Bela inter Somniani et Bela, *Rechinger 27553* (G, W); Inter Damloti et Khadiji, *Rechinger 28511* (G, W).

8ab. Var. **tuberculosum** (Boiss.) Kazmi, comb. nov.

Heliotropium undulatum Vahl var. *tuberculosum* Boiss. Diagn. Pl. Orient. 1(2): 89. 1849.
H. tuberculosum (Boiss.) Boiss. Fl. Orient. **4**: 147. 1875.
H. kotschyi Bunge, Reliq. Lehmann 404. 1851.
H. bacciferum Forssk. subsp. *tuberculosum* (Boiss.) H. Riedl, Oesterr. Bot. Zeitschr. **113**: 165. 1966; in Rechinger, Fl. Iranica **48**: 20. 1967.

TYPE: Insula Khark in sinu Persico, *Kotschy 22* (W).

Leaves usually terete or subterete, up to 10(–20) mm. long, 2–3 mm. broad, covered on both surfaces mostly with stout hairs arising from large white tuberculate bases.

West Pakistan: KARACHI DIST.: Clifton, shrub, 1/2 ft. tall, leaves falling towards the base, *Jafri 1401* (E); Bela, Uthal to Naka Kharai, *Lamond 229* (E); *Rechinger 27474* (G, W); Karachi, *Rehman* in *R. R. Stewart 25721* (BM); *Nath & Samson 15320* (GH); *Nath 15277* (GH). MAKRAN DIST.: Inter Kappar et Gwader, *Rechinger 27898* (G, W); *Kazmi 2495* (PES). Miscellaneous: Sind, *Herb. Ind. Or. Hook. f. & Thoms., Stocks 9* (K); *Cooke s.n.* (K).

Both varieties of subspecies *bacciferum* are distributed from Morocco to West Pakistan on the southern side of the Mediterranean. Variety *tuberculosum* is more common near the sea coasts, while var. *bacciferum*

is usually found in the inland areas. A number of intermediate forms are common all over the area of distribution of the subspecies. Both varieties bear trichomes which arise from tuberculate bases, but such trichomes are less common in var. *bacciferum* than in var. *tuberculosum*. The type of trichome has no relation to the form of the leaves, which is the major distinguishing character of the two varieties.

8b. Subsp. **lignosum** (Vatke) Kazmi, comb. nov.

Lithospermum lignosum Schweinf. ex Vatke, Oesterr. Bot. Zeitschr. **25:** 167. 1875.
H. lignosum Schweinf. ex Vatke, *loc. cit.* 1875.

TYPE: Arabia: Ras Ranar, *Schweinfurth 2111* (B).

Nutlets usually joined in pairs, pairs winged at the separating margins, wings narrow; the line of separation of the two nutlets is conspicuous.

DISTRIBUTION OF SUBSP.: Arabia, West Pakistan, and Egypt(?).

8ba. Var. **lignosum.**

Leaves usually short and terete, sometimes flat and lanceolate, 6–20 mm. long, 3–4 mm. broad, at times lower cauline leaves are broad and the upper short and narrow, covered on both surfaces with hairs arising from white tubercles. The line of separation of the two nutlets in a pair is more conspicuous than in var. *fartakense*, sometimes deeply grooved.

West Pakistan: KARACHI DIST.: Karachi, between Mango Pir and Band Murad, *Jafri 1353* (E); Hawkes Bay, flower white with yellow eye, *Burtt 1561* (E). MAKRAN DIST.: between Pasni and Kappar, on Pasni-Gwader Road, *Kazmi 1031* (PES); *Lamond 456* (E); Ras Nuh, south of Gwader, rocky top of cliff promontory, flower white, 100–150 m., *Lamond 483* (E).

8bb. Var. **fartakense** (O. Schwartz) Kazmi, comb. nov.

H. fartakense O. Schwartz, Mitt. Inst. Allg. Bot. Hamburg **10:** 207. 1939; Riedl in Rechinger, Fl. Iranica **48:** 20. 1967.

TYPE: Arabia: Kustengebiet von Hadramaut auf Dünensand bei Ras Fartak, *Poulay s.n.* (HBG).

Lower cauline leaves lanceolate, tapering at both ends, up to 6 cm. long and 1 cm. broad, upper cauline leaves shorter and narrower; both surfaces uniformly covered with short white trichomes, arising from white tuberculate bases, nerves sunken and glabrous on the upper surface, prominent and densely covered with long trichomes on the lower surface. The line of separation of the two nutlets in a pair is less conspicuous than in variety *lignosum*.

West Pakistan: KARACHI DIST.: Karachi, *Rich 437* (K); *Cooke* (Dec. 1892) *s.n.* (K). MAKRAN DIST.: Inter Pasni et Kappar, *Kazmi 1026* (PES); *Rechinger 27867* (G, W).

Subspecies *lignosum* is distributed at the eastern end of the range of *Heliotropium bacciferum*. It is differentiated from the typical subspecies by the narrower wings of its seeds and by the very slightly to deeply grooved line of separation between the nutlets in a pair. On ripening of the fruits the nutlets are always separated in variety *lignosum* and usually are in variety *fartakense*. Rarely in variety *fartakense* (*Rich 437*) do the nutlets remain united even on the complete ripening of the fruit, as they do in subspecies *bacciferum*. In the form of leaves the varieties of subspecies *lignosum* differ as do those of subspecies *bacciferum*, and here also many intermediate forms are found. All the four varieties are related in the coherence of the nutlets, from being united to being free in the following sequence: *tuberculosum*, *bacciferum*, *fartakense*, and *lignosum*. In the form of leaves and in habit, variety *lignosum* is closely related to variety *tuberculosum*, and variety *bacciferum* to variety *fartakense*.

9. **H. dasycarpum** Ledeb. in Eichw. Pl. Nov. Iter Casp.-Cauc. 11. 1831–33; DC. Prodr. **9**: 535. 1845; Boiss. Fl. Orient. **4**: 140. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 148. 1883; Burkill, Fl. Pl. Baluchistan 50. 1909; Riedl in Rechinger, Fl. Iranica **48**: 23. 1967.

TYPE: Prope Krasnovodsk, *Eichwald s.n.* (LE).

Perennial herb or undershrub, erect, up to 45 cm. tall, profusely and usually divaricately branched, stem and branches densely covered, with adpressed, or sometimes with spreading, white trichomes not arising from white tuberculate bases, or sometimes intermixed with scattered short trichomes arising from minute tuberculate bases. Leaves lanceolate to ovate, including petioles up to 40 mm. long, to 15 mm. broad, lower and middle cauline leaves with longer petioles, petioles up to 15 mm. long, upper cauline leaves usually with shorter petioles or sometimes subsessile or rarely sessile; nerves on the upper surface sunken and not prominent, on the lower surface raised and prominent; upper surface covered with short simple trichomes mixed with a few arising from minute tuberculate bases, lower surface usually more densely covered with a mixture of short and rather longer trichomes arising from tuberculate bases than the upper surface; margins usually revolute; apices round, obtuse or rarely subacute. Inflorescence usually terminal, loose with few distant, sessile, or at fruiting time, subsessile to very short pedicellate flowers. Calyx divided nearly to the base, lobes lanceolate to ovate-lanceolate, 1.8–2.8 mm. long, 0.7–1 mm. broad, usually acute, hairy outside, with spreading trichomes. Corolla subtubular, narrowed slightly at the throat, externally silky hairy, glabrous inside, 2–3 mm. long; corolla tube 2.5–3 mm. long, lobes 0.7–1 mm. long, inflexed at 1/2–1/3 of their length, sinuses entire, narrow. Anthers linear-oblong, emarginate at the bases, sessile, inserted 1 mm. above the base of corolla, 1.2–1.5 mm. long. Stigma 1 mm. long, cylindro-conical with prominent disc, glabrous or slightly puberulous, usually with longer trichomes at the tip; style much shorter than the stigma. Fruits

globose, up to 2.5 mm. in diameter, when young covered with long silky trichomes, becoming glabrous; nutlets 4, free, dark brown to black.

DISTRIBUTION OF SPECIES: Iran and adjoining areas of URSS, Afghanistan, South Siberia, and West Pakistan.

9a. Var. **dasycarpum.**

Stem and branches densely covered with white trichomes, usually not arising from tuberculate bases or sometimes intermixed with a few which do so. Leaves mostly tapering at both ends. Calyx lobes broader and corolla lobes shorter than those of var. *gymnostomum.*

West Pakistan: KALAT DIST.: Mastung, 1840 m., *Jafri & Akbar 1714* (E); *G. Popov 292* (BM); Mastung on the way to Spin Blundi, 1800 m., *Jafri & Akbar s.n.* (E). QUETTA DIST.: Quetta, Sariab road, 5 km. from center, weed of vineyards, 1700 m., *Kazmi 1441B* (PES); *Lamond 927* (E, G); *Rechinger 28831* (G, W); Kach, *R. R. Stewart 549* (MICH).

9b. Var. **gymnostomum** (Hemsl.) Kazmi, comb. nov.

H. gymnostomum Hemsl. in Hook. Icon. **18:** *t. 1755.* 1883.

TYPE: Gilgit Expedition, Roshan at 10,000 ft., *Dr. Giles s.n.* (K).

ICON.: Hemsley, *l.c.* 1883.

Stem and branches usually covered thinly with scattered short, spreading hairs, usually arising from tuberculate bases, older stems sometimes glabrous below. Leaves usually ovate, not much attenuated towards the base, sometimes truncate. Calyx lobes narrower and corolla lobes longer than in var. *dasycarpum.*

West Pakistan: GILGIT AGENCY: Gilgit valley, 1300–1800 m., *Duthie* (30. 7. 1892) *s.n.* (K); Gilgit Expedition, *Giles* (marked = *Griffith* No. 585) *s.n.* (E); Gilgit, river terrace, poor sandy soil, irrigated and cultivated area, flowers cream-yellow, 1580 m. *Polunin 6025* (E); Gilgit in deserts, 1800 m., *R. R. Stewart 16196* (A); Gilgit, watershed Gilgit river, *Giles 239* (K); Astor, *Duthie 12293* (K).

In the original description of Ledebour the nutlets of *Heliotropium dasycarpum* are cited as being glabrous, other authors described the nutlets as glabrous or as hairy. Most of the specimens examined by me from West Pakistan and other areas of the distribution of the variety have long silky trichomes which, in some cases, especially in fully ripe and old nutlets, have fallen off. Hemsley, in his description of *H. gymnostomum*, incorrectly considered the silky trichomes of the nutlets as the part of the corolla tube remaining attached to the fruit. The important distinguishing character of *Heliotropium dasycarpum* is its very short, more or less glabrous style, which is much shorter than, or hardly reaching 1/5–1/3 of the length of the stigma. The specimens cited under variety *gymnostomum*, mostly from northern West Pakistan, are thinly covered with crisped, short trichomes, mostly spreading and almost arising from

minute tuberculate bases. These trichomes sometimes fall along with the calcareous discs (in age), leaving the lower stems quite glabrous, which is not the case in variety *dasycarpum*. Moreover, the leaves of variety *gymnostomum* are ovate and sometimes truncate at the base in comparison with leaves of variety *dasycarpum* which are usually tapering at both ends. Similarly, the Gilgit specimens have longer and narrower corolla lobes in comparison with those of specimens from Baluchistan.

10. **H. brahuicum** Stocks in Hook. Jour. Bot. 4: 173. 1852.

H. rechingeri H. Riedl in Rechinger, Fl. Iranica **48**: 25. 1967, *syn. nov.*

TYPE: Upper Beloochistan, about 4,000 ft., *Stocks 865* (K).

ICON.: Rechinger, Fl. Iranica **48**: *t. 8.* 1967, under *H. rechingeri.*

Perennial herb or undershrub up to 30 cm. tall; stems many, branched; stem and branches covered with appressed, antrorse or erect white trichomes, mostly arising from small tuberculate bases. Leaves petiolate, petioles 3–10 mm. long, longer in middle cauline leaves; lamina ovate, acute or obtusish, usually truncate at base, sometimes attenuate, nerves inconspicuous on the upper surface, prominent below, upper surface covered with thin short trichomes, lower surface densely covered with longer ones; margins usually subrevolute, 7–20 mm. long, 6–14 mm. broad. Inflorescence usually terminal, lax, flowers subsessile or sessile, lower old flowers or fruits 5 mm. apart, shortly pedicellate; pedicels up to 1.5 mm. long. Calyx 2.5(–3) mm. long, divided to the base, lobes lanceolate, acute, covered on the upper surface with few hairs, more densely so on the margins, trichomes sometimes hooked at their tips. Corolla ca. 5 mm. long, tubular, pallid, externally covered with thin, short, silky, retrorse trichomes, glabrous within, lobes 0.9–1.2 mm. long, 0.5–0.6 mm. broad at bases, obtusish, incurved at about 2/3 of their length, sinuses between the lobes broad, sometimes lobed or slightly dentate. Anthers oblong to linear-oblong, bases more or less roundish 1.6–2 mm. long; sessile, inserted 1.8–2 mm. above the corolla base. Stigma conical to conical-oblong, 1–1.4 mm. long, stigmatic ring 0.6–0.7 mm. in diameter, slightly puberulous with longer trichomes at the top; style retrorse strigose, 0.8–1 mm. long. Ovary glabrous. Fruits not seen.

DISTRIBUTION: West Pakistan.

West Pakistan: KALAT DIST.: Dasht Baddoo near Kalat, 1900–2000 m., *R. R. Stewart 744* (MICH); Mastung, *M. A. Siddiqui 1948* (K). PISHIN DIST.: Pishin, *Lace s.n.* (E, K). QUETTA DIST.: Ad radices occidentalis montium Chiltan inter Dulai et Kanak, substr. calc., 1600 m. *Rechinger 29115* (G, W); *Kazmi 1550A* (PES); Quetta, Glouchester (Gloucester) Road, *Santapau 6285* (GH). Miscellaneous: Upper Baluchistan, above 1300 m., *Stocks 865* (K).

Heliotropium brahuicum is closely related to *H. dasycarpum* from which it is distinguished by its narrower corolla lobes with broad sinuses. The sinuses are usually 1–3-lobed, sometimes minutely dentate, and rarely

entire. The style of *H. dasycarpum* is glabrous and always shorter than the stigma but the style of *H. brahuicum* equals the stigma in length and has prominent retrorse trichomes.

The specimens cited under *Heliotropium rechingeri* agree in all details with *H. brahuicum* and simply represent the more pubescent form with leaves not or slightly undulate at the margins.

11. **H. gillianum** (H. Riedl) Kazmi, comb. nov.

H. popovii H. Riedl subsp. *gillianum* H. Riedl in Rechinger, Fl. Iranica **48**: 27. 1967.

TYPE: Afghanistan: North Herat, 490 m., *Gilli 3106* (W).

Perennial herb, branched from the base, base sublignose; stem 30–40 cm. tall; stem and branches densely covered with thin, appressed, up to 1 mm. long trichomes intermixed with some spreading ones arising from minute tuberculate bases. Leaves petiolate, petioles 2–10 mm. long; lamina broad ovate, obtuse to acutish, bases truncate 6–20 mm. long, 5–15 mm. broad; margins crenulate to somewhat undulate and slightly revolute; upper surface covered with thin, appressed trichomes up to 0.2 mm. long, arising from minute tuberculate bases, these denser along the sunken nerves, mixed with sparsely scattered white trichomes up to 0.5 mm. long, arising from comparatively larger tuberculate bases, lower surface densely covered with trichomes 0.3–0.7 mm. long, becoming longer on the raised nerves. Inflorescence terminal or axillary, simple or geminate, 3–15-flowered, when young contracted, later elongate with lower flowers 3–5 mm. apart. Calyx sessile, ca. 3 mm. long, divided to the base; lobes lanceolate to ovate-lanceolate, acute, spreading, falling with the fruits, externally densely covered with white hairs. Corolla tubular, exceeding the calyx, 4–5(–5.5) mm. long, outside densely covered with retrorse trichomes, inside hairy above the anthers and usually along the nerves which alternate with the stamens; lobes 1–2 mm. long, sublinear with plicate aestivation, acute, inflexed at 1/2–1/3 of their length. Anthers 1.5–2 mm. long, broadly cordate at base, gradually narrowed towards the subacute apices, sessile, inserted 1.5–2 mm. above the corolla base. Stigma conical-elongate, hispid at apex, up to 1.5 mm. long. Style slightly hairy, 0.7 mm. long. Nutlets ovoid, convex dorsally, smooth, glabrous, 2 mm. long.

DISTRIBUTION: Iran, Afghanistan, W. Pakistan.

West Pakistan: CHAGHI DIST.: 20–30 km. E. Mirjaveh, in deserto, *Rechinger 27256* (G, W); 100–150 km. E. Nok Kundi, *Rechinger 27273* (G, W).

Heliotropium gillianum may be easily distinguished from other closely related species with inflexed corolla lobes in West Pakistan where this species is the only one of the group having internally hairy corollas. The two specimens cited above were cited under *H. taftanicum* Rech. f., Aellen & Esfand. by Riedl in Rechinger, Fl. Iranica **48**: 25. 1967. On

dissecting the flowers, I found, however, that they represent *H. gillianum*.

Heliotropium gillianum is based on *H. popovii* H. Riedl subsp. *gillianum* H. Riedl and is distinguished from the typical subspecies by having longer corolla lobes inflexed at their apices, and internally hairy corollas. In *H. popovii* the corolla is glabrous within, its lobes do not exceed 0.7 mm. in length, and they are not inflexed at their apices. *Heliotropium popovii*, which is based on *H. gymnostomum* M. Pop. Acta Horti Petrop. 42: 239. 1931, non Hemsl. 1883, and variety *aucheriiforme* M. Pop. also differ from *H. gillianum* in the size of leaves, petioles, and flowers and in the pubescence of stem and leaves. *Heliotropium gillianum* seems, therefore, to merit specific recognition.

12. **H. lamondiae** Kazmi, sp. nov.

TYPE: West Pakistan, Baluchistan, Chagai, 20–30 km. E. Mirjaveh, desert, *Jennifer Lamond 134* (E-holotype).

Herba perennis, basi lignosa, pluricaulis, a basi ramosissima, erecta vel ascendens, 15(–30) cm. alta. Caulis ramique pilis ad summum 1 mm. longis appressiusculis vel ± patentibus interdum tuberculo minutissimo insidentibus densissime hirsuti. Folia omnia brevi-petiolata, petiolo 1–4 mm. longo, lamina 3–12(–15) mm. longa, 3–12(–14) mm. lata, late ovata, obtusa vel rotundata, basi truncata, margine crenulata revoluto, nervi supra valde impressi subtus prominentes, supra viridia plerumque appressissime pilosa, pilis 0.3–0.4 mm. longis, nonnunquam etiam pilis longioribus, 0.5–0.7 mm. longis intermixtis, subtus densissima albidi- vel canescenti-pilosa in sicco coriacea. Inflorescentiae terminales vel axillares, simplices, 3–7-florae, primo valde contractae demum elongatae, usque 3 cm. longae. Calyces sessiles vel subsessiles, ± 2 mm. longi, laciniis 5, usque ad basin liberis, lanceolatis, ± acutis, densissime subappressiusculis vel patulae albo-pilosis. Corolla tubulosa, pallida, 3–3.5 mm. longa, extus dense retrorse pilosa intus glabra, lobis triangularibus, subacutis, 0.5 mm. longis, 0.5 mm. ad basin latis, in sinubus inter lobos dentibus acutis, brevissimis 0.1 mm. longis distinctis praedita. Antherae oblongae, 1.6 mm. longae, a basi latissime cordatae, apice versus attenuatae; connectivum parve productum, hamato-incurvatium, 1–1.5 mm. supra basin corollae insertum. Stylus 0.3–0.5 mm. longus, pilosus. Stigma conicum, 0.5–0.7 mm. longum ad apicem pilosum. Nuculae ovoideae 2.5 mm. longae, primo albo-sericeae demum glaberrimae, purpureo-flavescentes.

DISTRIBUTION: West Pakistan.

West Pakistan: CHAGAI DIST.: 20–30 km. E. Mirjaveh, desert, *Lamond 134* (E).

Heliotropium lamondiae is closely related to *H. aucheri* from which it differs in having shorter and broader leaves, shorter calyx and corolla lobes. The corolla lobes of *H. aucheri* are linear with narrow and entire sinuses 0.8–1 mm. long, while those of *H. lamondiae* are triangular and do not exceed 0.5 mm. in length, with sinuses obviously lobed or dentate.

Heliotropium lamondiae has anthers about one and a half times longer than those of *H. aucheri*.

13. **H. aucheri** DC. Prodr. **9**: 533. 1845; Boiss. Fl. Orient. **4**: 143. 1875; Riedl in Rechinger, Fl. Iranica **48**: 26. 1967.

H. sericocarpum Bunge, Bull. Soc. Nat. Moscou, **42**(1): 322. 1869.

TYPE: Prope Mosul, *Aucher s.n.* (G).

Perennial, erect or suberect herb with many flexuose stems; stem and branches covered with short, appressed or subappressed, white trichomes intermixed with longer, stiff, spreading ones up to 1.5 mm. long. Leaves petiolate, ovate or orbicular, sometimes subcordate at the base, up to 25 mm. long, 15–20 mm. broad, upper surface covered with ± adpressed short, white, thin trichomes intermixed with longer and thicker ones arising from tuberculate bases, lower surface densely hairy; margins crenulate, revolute. Inflorescence usually solitary, sometimes geminate, short with few distant flowers. Calyx divided to the base, lobes linear, obtuse, hairy, ca. 2.5 mm. long. Corolla subtubular, covered externally with retrorse silky short trichomes, glabrous inside 3–3.5 mm. long; lobes linear, acute, inflexed when young, later spreading, 0.8–1 mm. long. Anthers 1 mm. long, oblong, sessile, connectives produced at apices and recurved, inserted about 1–1.3 mm. above the corolla base. Style 0.7 mm. long, with retrorse thin trichomes. Stigma more or less equalling the style, conical-elongate, hairy at apex. Fruits covered with white trichomes.

DISTRIBUTION: Iraq, southern and central Iran, and West Pakistan.

West Pakistan: KALAT DIST.: Kalat, 1200 m. *McCann 394, 402* (BM).

14. **H. cabulicum** Bunge, Bull. Soc. Nat. Moscou **42**(2): 328. 1869; Boiss. Fl. Orient. **4**: 143. 1875; Burkill, Fl. Pl. Baluchistan 50. 1909; Riedl in Rechinger, Fl. Iranica **48**: 29. 1967.

TYPE: Afghanistan, *Griffith 5930* (K).

Perennial, usually with many stems arising from a woody base, erect, 30–40(–45) cm. tall; stems green, much branched, branches straight or flexuose, covered thinly with short, usually antrorse, crisped trichomes up to 0.7 mm. long, arising from minute tuberculate bases. Lower cauline leaves very short petiolate, middle and upper ones usually sessile or subsessile, lanceolate to ovate-lanceolate, obtusish to acute, up to 30 mm. long, up to 17 mm. broad, nerves on the upper surface ± sunken, less conspicuous, those on the lower surface raised; upper surface covered with distant short, ± erect trichomes usually arising from tuberculate bases, lower surface sometimes ± glabrous, except on nerves; margins entire, often slightly revolute. Inflorescence usually terminal, solitary or geminate, 3–7-flowered, short when young, later elongated with flowers up to 7 mm. apart. Calyx usually sessile or sometimes pedicellate, pedicels 2–3 mm., rarely up to 10 mm. long, lobes free to the base, ovate-

lanceolate, gradually tapering towards the acute apices, externally thinly covered dorsally and thickly at the margins with short trichomes, up to 0.5 mm. long, usually arising from tuberculate bases, lobes 3–3.5(–4) mm. long, 1.3–1.5 mm. broad. Corolla 6–8 mm. long, infundibular, externally covered with spreading trichomes, denser on veins, comparatively softer and longer trichomes within from the bases of the anthers to the tips of the corolla lobes, dense at throat and veins; corolla tube ± 6 mm. long, lobes 1.5–2 mm. long and broad, roundish, undulate at margins, spreading. Anthers ovate, sessile, roundish or subcordate at the bases, gradually attenuated towards the apices, 1.5–1.7 mm. long, inserted about 1 mm. above the corolla base. Stigma pyramidal, glabrous, subsessile 0.7–0.8 mm. long, 0.7–0.8 mm. in diameter. Fruits glabrous, dark brown, 2 mm. high, 2–2.5 mm. in diameter.

DISTRIBUTION: Afghanistan and West Pakistan.

West Pakistan: KURRAM AGENCY: Parachinar, 1–10 km. E. of town, roadside, shingle plain, 1500 m., *Lamond 1892* (E); Thal to Parachinar, roadside slope, flowers white, *Lamond 1869a* (E); *Rechinger 30886* (G, W); Inter Amal Kot et Sadda, in glariosis, 1500 m., *Rechinger 30959* (G, W); Kurram valley, *Afandi 313* (PES). WAZIRISTAN AGENCY: Waziristan, Wana, 1580 m., open hillside, *D. Lowndes 1661* (E). Miscellaneous: Kabul to Jamrud, *Aitchison 235* (E).

15. **H. ulophyllum** Rech. f. & H. Riedl in Rechinger, Fl. Iranica **48**: 31. 1967.

TYPE: West Pakistan: In parte inferiore faucium Torkhan supra Harnai, 900 m. 14. 5. 1965, *Rechinger 29487* (W).

Perennial with woody base, erect, 30–45 cm. tall; stem and branches densely covered with white short (0.2–0.3 mm. long), crisped, rigid, usually spreading or sometimes ± retrorse trichomes, arising from minute tuberculate bases. Cauline leaves petiolate, petioles 1–6 mm. long; lamina 10–40(–45) mm. long, (4–)6–25 mm. broad, ovate to oblong-ovate or oblong-lanceolate, obtuse to acutish, oblique towards the petiole, rarely subhorizontally truncate; margins undulate to crisped-undulate, slightly revolute, nerves on the upper surface inconspicuous, prominent below, upper surface thinly, lower surface densely clothed with trichomes like those of the stem; upper cauline leaves like the lower but shorter, narrower, and sessile. Inflorescence lax, bearing up to 12 flowers, solitary or geminate. Calyx subsessile or sessile, 3.5–4 mm. long, divided to the base, lobes lanceolate, acute, covered externally with spreading trichomes denser on the margins, and within with longer, thinner, appressed trichomes. Corolla infundibuliform, ca. 5 mm. long, with short, subpatent, ± retrorse hairs outside, glabrous within, tube 3.5–4 mm. long, lobes 1–1.5 mm. long and broad at bases, rotund, slightly lobed or crisped at margins, patent. Anthers sessile, oblong, slightly cordate at base, gradually attenuated towards the apices, ca. 2 mm. long, inserted 1 mm. above the base of corolla. Style glabrous 0.4–0.5 mm. long; stigma conical 0.8–0.9 mm. long. Immature fruits glabrous, smooth.

DISTRIBUTION: West Pakistan.

West Pakistan: QUETTA DIST.: Loralai to Harnai, below Torkhan Pass, near Harnai, 900–1400 m., *Kazmi 1699A* (PES); *Lamond 1274* (E); *Rechinger 29487* (W).

Heliotropium ulophyllum resembles *H. cabulicum* from which it is distinguished in having the calyx nearly equalling the corolla tube, the shorter corolla glabrous within, and longer anthers.

16. **H. remotiflorum** Rech. f. & H. Riedl in Rechinger, Fl. Iranica **48**: 35. 1967.

TYPE: West Pakistan: Makran, Sunster versus Kikki, 17. 4. 1965, *Rechinger 27990* (W-holotype, G-isotype).

ICON.: Rechinger, Fl. Iranica **48**: *t. 10.* 1967.

Annual (?) or perennial, erect or suberect, much branched, branches long, slender. Stem and branches covered with short, appressed hairs up to 0.3 mm. long, intermixed with scattered thick, spreading straight or slightly curved trichomes arising from large tuberculate bases and up to 0.7 mm. long. Leaves petiolate, petioles up to 7 mm. long, hairy, lamina ovate, up to 13 mm. long, and 7 mm. broad, apices obtuse or roundish, bases round or sometimes truncate, margins entire, sometimes slightly revolute, nerves inconspicuous or sunken on the upper surface, prominent and raised below, upper surface ± rugose, covered uniformly with very short (to 0.2 mm. long) trichomes, lower surface with longer ones up to 0.5 mm. long, denser on the nerves, arising from conspicuous tuberculate bases. Inflorescence terminal or axillary, usually geminate sometimes solitary, short when young, later elongate, up to 12 mm. long with flowers 1–5 mm. apart. Calyx usually subsessile or the lower flowers pedicellate (pedicels up to 1.5 mm. long), divided to the base, lobes ovate to broad-lanceolate, obtusish, in fruit patent, persistent, later deciduous, 2–2.5 mm. long, 0.6–0.8 mm. broad. Corolla externally covered with short, silky, retrorse trichomes, internally papillose at the constricted throat 2.5(–3) mm. long, lobes narrow, obtuse, plicate, inflexed when young, later patent, ca. 1 mm. long, 0.5 mm. broad at base. Anthers ovate, 1 mm. long, slightly bifid at apex, ± cordate at base; filaments 0.1–0.2 mm. long, inserted 0.6–0.7 mm. above the corolla base. Stigma sessile, glabrous, at apex bifid and hairy, 0.9–1 mm. long, 0.7–0.8 mm. in diameter at the base. Fruits 1.7 mm. high, 1.8–2 mm. in diameter, lobed, nutlets coherent when young becoming free, covered with long silky trichomes, dark brown to blackish.

DISTRIBUTION: West Pakistan.

West Pakistan: MAKRAN DIST.: Sunster versus Kikki, *Rechinger 27790* (G, W); Inter Gwader et Sunster, *Rechinger 27972* (W); inter Pasni et Kappar, *Rechinger 27875, 27884* (G, W); between Kappar and Gwader, *Kazmi 1036* (PES); 90–100 km. S. Turbat versus Pasni, *Rechinger 27847* (W).

17. **H. baluchistanicum** Kazmi, sp. nov.

TYPE: West Pakistan: Baluchistan: Mir Ali Khel, 1200 m., 17. 5. 1896, *Duthie 18922* (K-holotype).

Perennis, basi lignescens, 15–25 cm. alta. Caules ad basim ramosi, ramis elongatis pilis tenuibus, crispis, adpressis vel patulis, brevioribus vel usque ad 1.2 mm. longis, densis obsitus. Folia inferiora longius vel superiora brevius petiolata, petiolis 2–10 mm. longis, lamina 10–25 mm. longa, 10–20 mm. lata, late ovata, basi late cuneata vel truncata, nervis supra impressis, subtus parve prominentibus, apice plerumque rotundata vel interdum parve obtusiuscula, margine integra haud revoluta, coriacea, colore sordide saepe brunnescenti- vel canescenti-viridi, indumento e pilis brevibus usque ad 1 mm. longis, crispis et glandulosis numerosis et pilis eglandulosis in pagina superiore dense, in pagina inferiore longioribus usque ad 1.5 mm. longis, multo dense, patule consistente. Inflorescentiae juveniles contractae demum paulo elongatae usque ad 5(–6) cm. longae, terminales vel axillares; plerumque geminatae vel rarissime solitariae, ebracteatae, floribus haud distantibus. Calyces sessiles vel rarissime inferiores subsessiles, 4–5 mm. longi, indumento ut in caule ad basin in laciniis 5 anguste linearibus, 0.5 mm. vix latis, obtusis divisi, post florendum persistentes. Corolla 6.5–7.2 mm. longa, anguste tubulosa, extra dense, patule tomentella, lobis 5 minutis, aestivatione a latere plicatis, suberectis, triangularibus vel late subrotundatis, usque ad 0.5 mm. longis, a basi 0.6–0.7 mm. latis, intus altero annulo pilorum super antheras, altero in fauce ornata, zona pilosa 1–1.5 mm. lata, pilis ca. 0.5 mm. longis, zona glabra 1–1.5 mm. lata. Antherae 1.5–1.7 mm. supra basin corollae sessiles, 1 mm. longae, oblongae, connectivum parve productum, rectum, acutae, basi rotundatae. Stigma 0.6–0.7 mm. longum, basi discoideum fere diametro appresso-conicum, apice rotundatum, glabrum; stylus 0.5 mm. longus, crassus, glaber. Ovaria glabra. Nuculae 2.2 mm. longae, 1.1 mm. latae, ovoideo-oblongae, dorso valde convexae, apicem productae, glaberrimae, flavae vel fuscae.

DISTRIBUTION: West Pakistan.

West Pakistan: Baluchistan, Mir Ali Khel, 1200 m., *Duthie 18922* (K).

Heliotropium baluchistanicum resembles *H. biannulatum* and also *H. dicriophorum* Rech. f. & H. Riedl (Biol. Skr. 13(4): 186. *fig. 142.* 1963), a species described from Afghanistan. It is well distinguished from *H. biannulatum* by having two rings of hairs inside the corolla, above the anthers and below the corolla lobes, distinctly separated by a glabrous zone (see observations under *H. biannulatum*) and from *H. dicriophorum* by having very short and broad corolla lobes not exceeding 0.5 mm. in length, and much shorter (only up to 1 mm. long) anthers. It also differs from both these species in the pubescence of stem and leaves. The trichomes in *H. baluchistanicum* are very long and crisped in comparison with the other two species.

18. **H. biannulatum** Bunge, Bull. Soc. Nat. Moscou **42**(2): 300. 1869; Boiss. Fl. Orient. **4**: 135. 1875; Riedl in Rechinger, Fl. Iranica **48**: 36. 1967.

H. khyberianum Rech. f. & H. Riedl in Rechinger, Fl. Iranica **48**: 35. 1967, *syn. nov.*

TYPE: In regno Cabulico, *Griffith 5933* (GH, K, P, W).

Perennial, erect, 20–30(–35) cm. tall, usually many stems arising from a woody base, stems branched, stem and branches grayish white, covered densely with thin, short, ± appressed trichomes, not arising from tuberculate bases, intermixed with (up to 0.5 mm.) long ones. Leaves petiolate, petioles 0.5–20 mm. long, hairy; lamina usually ovate to ovate-oblong, up to 5 cm. long, up to 2.5(–3) cm. broad; nerves deeply sunken on the upper surface, prominent below, margins usually entire, rarely slightly undulate, apices usually obtuse, sometimes roundish, rarely acutish, bases usually attenuated towards the petioles, sometimes truncate or subcordate, upper surface densely and uniformly covered with thin, up to 0.5 mm. long, ± appressed trichomes, not arising from tuberculate bases, lower surface more densely hairy on nerves and veins, giving a honeycomb appearance. Inflorescence usually terminal, simple or geminate, up to 10 cm. long (remaining scorpioid even at fruiting), with closely set uniseriate flowers. Calyx sessile, persistent or rarely deciduous with the fruit, 3–5.5 mm. long, divided to the base, lobes linear, up to 0.7 mm. broad, obtuse to acutish, externally densely covered with ± patent trichomes up to 0.5 mm. long, erect, after fruiting wide open or sometimes reflexed. Corolla tubular, 5–7 mm. long, externally covered with short, usually retrorse, sometimes subpatent trichomes, densely hairy above the anthers and below the corolla lobes within, leaving a less or sparsely hairy zone in between, trichomes to 0.7 mm. long; corolla lobes 0.5–1.5 mm. long, 0.5–1.2 mm. broad, ovate or roundish, entire, imbricate, glabrous to puberulous inside, erect or patent. Anthers sessile, ovate-oblong, 1.2–1.3 mm. long, connectives very slightly produced, erect, acute, at bases roundish or slightly dilated, inserted ca. 2 mm. above the corolla base. Stigma 0.6–0.9 mm. long, compressed conical, round at apex, discoid at base, base 0.7 mm. in diameter, sometimes fleshy and slightly undulate, glabrous; style slender, glabrous 0.4–0.6 mm. long. Ovary glabrous, nutlets 4, free, glabrous, smooth or sometimes slightly punctate, acutish at apices, 1.4–1.6 mm. long, 0.8–1 mm. broad.

DISTRIBUTION: West Pakistan and Afghanistan.

West Pakistan: KHYBER AGENCY: Machi Kand, flowers yellow, *Nath* in *R. R. Stewart 15433* (GH); Jamrud, Bara Fort, gravel cliffs of dry nullah, flowers deep yellow, *Burtt 702* (E); in jugo Landi Kotal, 700–1000 m., *Rechinger 19368* (G, W); Tor Khama, ad confinis Afghaniae, 700 m., *Rechinger 30352* (G, W); Peshawar to Tor Kham, Khyber Pass, steep roadside slopes, shale, flowers golden yellow, 650–900 m., *Lamond 1586* (G, E); Khyber Pass, *Faridi s.n.* (MICH); *Kazmi s.n.* (PES); Tor Kham near Afghan-Pakistan border, *A. J. Ahmad 21* (PES). PESHAWAR DIST.: Peshawar, *J. L. Stewart 178* (GH).

The corolla of *Heliotropium biannulatum* is hairy within from above the anthers to the bases of the corolla lobes, but the length and density of the trichomes are not uniform throughout. The trichomes just above the anthers and just below the bases of the corolla lobes are longer and denser in comparison with those of the intermediate zone which is loosely and sparsely pubescent with usually short trichomes. Sometimes at a glance it appears, as it also does from the name *biannulatum*, that there are two rings of trichomes, but actually the two zones are not separated by a glabrous zone as in *H. baluchistanicum*, but are continuous with shorter and loose trichomes.

Heliotropium khyberianum has been distinguished from *H. biannulatum* by three characters, viz., two zones of trichomes separated by a glabrous zone, undulate margins of the stigmatic rings, and yellow flowers. As mentioned above, the density and length of the trichomes of the intermediate area inside the corolla of *H. biannulatum* are quite variable and *H. khyberianum* represents the plants which have comparatively shorter and less dense trichomes in the intermediate zone. The undulate margin of the stigmatic ring is also variable and is not confined only to the plants of Khyber Pass or *H. khyberianum*, but this variation is also found in the plants belonging to *H. biannulatum* from Afghanistan; moreover, this character can not be correlated with any other distinguishing characteristic. I did not find, in any description, or in a note on any sheet, remarks concerning the color of the flower of *H. biannulatum*, but from the herbarium specimens I examined, they appear to be yellowish and therefore, not different from those of *H. khyberianum*.

19. **H. calcareum** Stocks, Hook. Jour. Bot. **4**: 174. 1852; Boiss. Fl. Orient. **4**: 128. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 150. 1883; Burkill, Fl. Pl. Baluchistan 50. 1909; Riedl in Rechinger, Fl. Iranica **48**: 42. 1967.

H. multiflorum Rech. f., Aell. & Esfand., Ann. Naturh. Mus. Wien **58**: 44. 1951; Riedl in Rechinger, Fl. Iranica **48**: 33. 1967, *syn. nov.*

TYPE: Hills of Scinde and lower Beluchistan, *Stocks 630* (K).

ICON.: Rechinger, Fl. Iranica **48**: *t. 5, fig. 1*; *t. 12, fig. 3*. 1967.

Annual, 30–40 cm. tall; stems single or many, arising from the woody base, erect or ascendent, branched, branches usually curved; stem and branches grayish, densely covered with up to 0.3 mm. long subappressed hairs, usually mixed with up to 0.6 mm. long, spreading hairs. Lower, middle, and sometimes even the upper leaves petiolate, petioles 10–20(–30) mm. long; upper and uppermost leaves sometimes subsessile; lamina oblong-ovate, ovate or broadly ovate, slightly attenuated, roundish or truncate at base, apices usually obtusish, sometimes roundish or acute; margins entire or subentire, sometimes revolute up to 5 cm. long, up to 3.5 cm. broad; nerves on the upper surface sunken, raised and prominent below; upper surface covered with white or grayish, thin (to 0.5 mm. long) hairs which are denser on the lower surface. Inflorescence short

when young, later elongated to 12 cm., usually geminate, spreading, many flowered. Calyx deciduous, sessile, divided to the base, lobes linear to oblong-lanceolate, acutish, 2–3 mm. long, 0.5–0.7 mm. broad, externally covered with patent ± antrorse white hairs, up to 0.5 mm. long, inside with longer and thinner trichomes. Corolla 3–4 mm. long, tubular, externally densely covered with retrorse, silky trichomes, glabrous within, corolla tube 2.5–3.5 mm. long, lobes roundish to broad ovate, entire, 0.4–0.5 mm. long, 0.5–0.7 mm. broad, rarely with minute intermediate lobes. Anthers sessile, oblong, slightly cordate at bases, gradually attenuated towards the acutish apices, ca. 1.5 mm. long connectives very slightly produced, sometimes curved inside. Style 0.1–0.5 mm. long, slightly hairy; stigma 1–1.2 mm. long, conical, bilobed, hairy at apex. Fruits globose, lobed, 1.5 mm. high, 2.5 mm. in diameter; nutlets covered with short, white, retrorse hairs, later becoming brown.

DISTRIBUTION: Iran and West Pakistan.

West Pakistan: DADU DIST.: 10–15 km. S. Sehwan, *Rechinger 28701, 28700* (G, W); *Kazmi s.n.* (PES); *Lamond 874, 874A* (E). KALAT DIST.: ca. 20 km. W. of Bela, W. of Jan Pass, rocky plateau, 300 m., *Lamond 310a* (E); *Rechinger 2760* (G, W); *Kazmi 916a* (PES); Jal Jhao to Awaran, roadside, mountain area of loose shale, *Lamond 334* (E); Jal Jhao, 400 m. *Rechinger 27667* (G, W). KARACHI DIST.: Near Thano Bulla Khan, stony hills, *Jafri 3710* (E). MAKRAN DIST.: Punjgur proper, 900 m. *Kazmi 1217* (PES); *G. Popov 197* (BM); 20 km. W. of Hoshab, rocky area, sandy soil, 100–200 m. *Lamond 388* (E); 10–30 km. S-W. of Turbat towards Gwader, 100–300 m. *Rechinger 27803* (G, W); *Lamond 423* (E); 30 km. S-W. Turbat versus Pasni, *Rechinger 27822* (G, W); Hoshab to Punjgur, south of Balagather plain, 8 km. from Hoshab, 600 m., *Lamond 533* (E); *Rechinger 28063* (G, W); W. Awaran versus Hoshab, *Rechinger 27693* (G, W); *Kazmi 974a.* (PES). QUETTA DIST.: Infra Mach, 600–800 m. *Rechinger 28774* (G, W); between Harnai and Wam Tangi, *Kazmi 1754* (PES); in alveo 8 km. N-W. Harnai, 900–1200 m. *Rechinger 29534* (G, W).

20. **H. europaeum** L. Sp. Pl. 130. 1753.

TYPE: "Habitat in Europa centrali" *Herb. No. 179. 8* (LINN).

Annual, stems sometimes woody at the base, usually branched below, erect, up to 45 cm. tall; stem and branches green to grayish green, densely covered with white subpatent hairs 2–10 mm. long, usually arising from minute tuberculate bases. Leaves petiolate, petioles of the lower leaves up to 4 cm. long, shorter in the upper leaves; lamina elliptic-ovate to obovate, slightly attenuate towards the base or truncate, apex obtuse to sometimes roundish, rarely acute, margins entire not revolute, 1–6 cm. long, 1–3.5 cm. broad; nerves on the upper surface inconspicuous, raised and prominent below; both surfaces covered ± uniformly, with white short (and sometimes longer), usually subpatent hairs, arising from minute but prominent tuberculate bases, longer hairs usually denser on the nerves of the lower surface. Inflorescence usually terminal, sometimes axillary, usually geminate, sometimes ternate, 2–5(–8) cm. long, with closely set

biseriate, ebracteate flowers or fruits. Calyx persistent, sessile, divided nearly to the base, lobes lanceolate, acuminate, erect or at fruiting patent, after falling of the fruits becoming reflexed, 2.5–3 mm. long, 0.5–0.8 mm. broad, densely covered with white, spreading trichomes up to 0.5 mm. long. Corolla 3–3.5 mm. long, tube cylindrical, more or less narrowed at the throat, externally hairy, inside glabrous, lobes suborbicular to subovate or rarely roundish, erect or spreading up to 1.5 mm. long, up to 1.2 mm. broad. Anthers sessile, gradually narrowed towards the acute apices, inserted 0.5–0.8 mm. above the corolla base, ca. 1 mm. long. Style absent to very short, stigmatic disc prominent, 0.4–0.6 mm. in diameter, stigmatic appendage subulate, usually hairy, rarely glabrous, slightly or deeply bifid at the apex, ca. 1 mm. long. Fruits globose, lobed, 1.5–2.2 mm. high and broad; nutlets 4, free, dorsally convex, ovate, glabrous to densely pilose, minutely verrucose to rugulose or rarely minutely tuberculate.

DISTRIBUTION OF SPECIES: From Europe to central Asia.

20a. Var. **europaeum.**

Calyx lobes up to 0.5 mm. broad, acute. Corolla tube not or only slightly narrowed at the throat. Stigmatic appendage deeply bilobed. Nutlets usually glabrous to sometimes pilose, usually rugulose to sometimes tuberculose.

DISTRIBUTION OF VAR.: Europe.

20b. Var. **lasiocarpum** (Fisch. & Mey.) Kazmi, comb. nov.

H. lasiocarpum Fisch. & Mey. Index Sem. Hort. Petrop. **4:** 38. 1837; DC. Prodr. **9:** 536. 1845; Riedl in Rechinger, Fl. Iranica **48:** 49. 1967.
H. tenuiflorum Bunge, Bull. Soc. Nat. Moscou **42**(2): 293. 1869, vix Guss.
H. eichwaldii Steud. var. *lasiocarpum* (Fisch. & Mey.) C. B. Clarke in Hook. f. Fl. Brit. India **4:** 150. 1883.
H. ellipticum var. *lasiocarpum* (Fisch. & Mey.) M. Pop. Acta Hort. Petrop. **42:** 220. 1931.

TYPE: "Penin. Dardscha" without citation of collector's name (LE-holotype, K-isotype).

Calyx lobes 0.5–0.8 mm. broad, acutish. Corolla tube narrowed at the throat. Stigmatic appendage more or less bifid. Nutlets usually densely retrorse pilose, rarely glabrous, minutely verrucose.

DISTRIBUTION OF VAR.: Transjordan, Syria, Iraq, Iran, Afghanistan, West Pakistan, Kashmir, India, Russia, and central Asia.

West Pakistan: ATTOCK DIST.: Campbellpur, *Rich 756* (K). BANNU DIST.: arenosis ad viam publicum, 400 m. *Rechinger 30042* (G, W). CHITRAL STATES: Shishi Col. N-E. of Drosh, 1800 m. edge of fields, *Stainton 3161* (BM, E). DADU DIST.: Sehwan, *Watt s.n.* (E). DERA ISMAIL KHAN DIST.: Tank, *Bennerji* in *Williams 7174* (GH, E); Dera Ismail Khan, on right side of Indus, *Schlagintweit 10810* (GH). GILGIT AGENCY: Gilgit, 1600 m., *R. R. Stewart 26194* (BM); North of Hindukush, *Giles s.n.* (E); near Gilgit, 1660 m., *McVean s.n.* (E); south of

Hindukush, 1830 m., *Giles 378* (K). GUJRANWALA DIST.: Khangah Dogran, *R. R. Stewart 1455* (K). JHELUM DIST.: Sangjoi near Jhelum, *R. R. Stewart 790* (K); Salt Range, Camp Choia Siadan Shah, *Bis Ram 450* (GH). KHAIRPUR DIST.: Khairpur Mirs, *Jafri 1023* (E). KALAT DIST.: Mastung, 1830 m., *Jafri & Akbar 1786* (E). KARACHI DIST.: Malir, *Jafri 835* (E); Karachi, *Stocks 457* (K). KHYBER AGENCY: Landi Kotal, 860 m., *Lowndes 1724* (E); *Kazmi s.n.* (PES); near Jamrud, *Kazmi 2483* (PES); Ali Masjid, *Kazmi s.n.* (PES). KOHAT DIST.: Kohat to Thal, ca. 20 km. from Kohat, ditch beside small hillock, 675 m. *Lamond 1557* (E). KURRAM AGENCY: Kurram valley, *Harsukh 14671* (K); Shalizan in dry stony soil, *Aitchison 662* (BM, GH); Parachinar, 1–10 km. E. of Town, roadside shingle plain, 1500 m., *Lamond 1882* (E). LAHORE DIST.: Walton near Lahore, 330 m. *R. R. Stewart 14719* (GH); Lahore, *L. S. Das* in Herb. *Lace 65* (E). MARDAN DIST.: Near Zaida, between Jahangira, weed of tobacco fields, flowers white or nearly so, *Burtt 618* (E). PESHAWAR DIST.: Shabkadar on Michni Road, *A. J. Ahmad 66* (PES); Peshawar 330 m., *R. R. Stewart 9077* (GH); *Kazmi 2493* (PES); *Schlagintweit 2632* (E); Peshawar-Charsadda Road, near Naguman bridge, weed of sugar cane fields, flowers white, *Burtt 976* (E). QUETTA DIST.: Sibi, *Lace 3886* (E); Jangal, 1500 m. *G. Popov 225* (BM). RAWALPINDI DIST.: Environ of Rawalpindi, 600–900 m., *Schlagintweit 10832* (BM); Sangla Hill by canal road, *R. R. Stewart 1424* (K); near Rawalpindi, 570 m., *Stocks 457* (K); *R. R. Stewart 13836* (GH); *Kazmi s.n.* (PES).

Kashmir: Environ of Srinagar, *Schlagintweit 4587* (BM, GH); Dal Lake, 1800 m. *R. R. Stewart 3339* (K); Srinagar, 1700 m. *Rich 1194* (K); Srinagar to Ganderbal, 1800 m. *R. R. Stewart* (GH); Bhimber, *Clarke 28125* (BM, K); Jhelum valley, Sumbal, 1730 m. *Ludlow & Sherriff 7710* (GH); vicinity of Pahlgam, on east of Lidder river, 27 miles N. of Islamabad, *Dickason 96* (MICH).

21. **H. ellipticum** Ledeb. in Eichw. Pl. Nov. Iter Casp.-Cauc. 10. *t. 4.* 1831–33; Riedl in Rechinger, Fl. Iranica **48**: 48. 1967.

H. eichwaldii Steud. Nomencl. Bot. ed. 2. **1**: 744. 1840–41; DC. Prodr. **9**: 535. 1845.

H. littorale Stev. Bull. Soc. Nat. Moscou **24**(1): 565. 1851.

TYPE: Turcomania: Ad litus orientale maris Caspii prope Krasnowodsk, *Eichwald* (LE).

The only way in which *Heliotropium ellipticum* differs from *H. europaeum* is in having comparatively broader sepals, gradually attenuated to the acute apices, and slightly reticulated, rugose, or indistinctly warted nutlets.

DISTRIBUTION: Armenia, Azerbaijan, Turcomania, Iran, and West Pakistan.

West Pakistan: Reported from Baluchistan: Loralai, Punjgur and Turbat, and from Waziristan: Dwa Warkha and Tank (Riedl. l. c. 1967).

I did not see any specimen of *Heliotropium ellipticum* from West Pakistan or Kashmir. The distinguishing characters given in the description indicate that this species is very close to *H. europaeum* var. *lasiocarpum*. On examining enough material it may prove to be a variety of *H. europaeum* or even identical to var. *lasiocarpum*.

22. **H. ovalifolium** Forssk. Fl. Aegypt.-Arab. 38. 1775; C. B. Clarke in Hook. f. Fl. Brit. India 4: 150. 1883; Cooke, Fl. Bombay Presidency 2: 211. 1908; I. M. Johnston, Jour. Arnold Arb. 32: 111. 1951.

H. kunzii Lehm. Icones 19. *t. 29.* 1821; DC. Prodr 9: 541. 1845.
H. syenites Spreng. Syst. 1: 539. 1825.
H. brocchianum Visiani, Pl. Aegypt. et Nubia 8. *t. 2. fig. 1.* 1836; DC. Prodr. 9: 541. 1845, *in syn.*
H. ambiguum DC. Prodr. 9: 533. 1845.
H. coromandelianum Raddi ex DC. Prodr. 9: 533. 1845.
H. coromandelianum α obovatum DC. Prodr. 9: 541. 1845.
H. niloticum DC. *Ibid.*

TYPE: Hadie, *Forsskål, s.n.* (C).

Annual, ascending or sometimes decumbent, commonly branched below the middle 10–40 cm. tall; stems usually several, stem and branches covered with grayish indument of slender pallid trichomes. Leaves petiolate, petioles slender, 0.5–2 cm. long, sometimes those of the lower leaves even longer; lamina elliptic, obovate or oblanceolate, margins slightly revolute, apices roundish or obtuse, bases obtuse to acute, midrib conspicuous but veins rarely visible, covered on both surfaces with white, short, appressed trichomes, 1–3(–6) cm. long, 4–12(–27) mm. broad. Inflorescence ebracteate, slender, terminal, usually in pairs, sometimes solitary or ternate, 1–12 cm. long with very numerous crowded small flowers in two ranks, scorpioid. Calyx subsessile, divided to the base, 1.5–2 mm. long, lobes unequal, cuneate to broadly lanceolate or sometimes ovate, acute, covered with short, white, appressed trichomes. Corolla white, 2.5–3 mm. long, tubular, slightly narrowed at the throat, limbs campanulate, externally covered with short, white, antrorse hairs, internally, above the middle, with coarse short hairs, tube 1–1.5 mm. long, lobes 0.5–0.8 mm. long, 0.5 mm. broad, ovate-oblong, infolded in bud, later erect or patent. Anthers 0.5–0.6 mm. long, lanceolate, acuminate, inserted about 0.5 mm. above the corolla base. Style absent; stigma 0.3–0.4 mm. long, thick, about 0.3 mm. in diameter at base, conical, apically bidentate. Fruits rounded, about 1.5 mm. high, slightly pointed, with appressed short hairs, breaking up into 4 equal nutlets.

DISTRIBUTION: Africa, Arabia, West Pakistan, India, Indochina, and Australia.

West Pakistan: MIRPUR KHAS DIST.: Gadro, *Zaman & Hussain s.n.* (PFI–M); without locality, in Herb. Wight, *Stocks 548* (K).

The form and indumentum of the leaves in *Heliotropium ovalifolium* is very variable. It can easily be distinguished from the allied species by its unequal calyx lobes, internally hairy corolla, sessile stigma, and the shape of the leaves.

23. **H. curassavicum** L. Sp. Pl. 130. 1753; DC. Prodr. 9: 538. 1845.

H. glaucum Salisb. Prodr. 113. 1796.
H. glaucophyllum Moench. Meth. Suppl. 147. 1802.
H. chenopodioides Willd. Enum. Hort. Berol. 175. 1809.
H. curassavicum var. *obovatum* DC. Prodr. **9**: 538. 1845.
H. virens E. Mey. ex DC. *Ibid.*
H. curassavicum var. *virens* (E. Mey. ex DC.) DC. *Ibid.*

TYPE: "Habitat in Americæ," *Herb. No. 179.11* (LINN).

Perennial, halophytic, decumbent, up to 40 cm. high, stem and branches with leaves more congested in the upper part, hollow, fleshy, glabrous. Leaves pale, glabrous, linear-lanceolate, oblong-lanceolate or narrow spathulate, attenuated towards a short petiole, slightly dilated towards the base, apices usually round, rarely subobtuse; margins entire, nerves not conspicuous on either side, glabrous, coriaceous, up to 5 cm. long and 1 cm. broad. Inflorescence usually terminal, sometimes axillary, simple or geminate, short, scorpioid at flowering, later elongated, up to 6 cm. long, with ebracteate, usually uniseriate, sometimes biseriate flowers or fruits. Calyx persistent, usually sessile, sometimes subsessile, divided nearly to the base, lobes ca. 1.5 mm. long, fleshy, broad lanceolate, obtuse, glabrous, not enlarged at fruiting. Corolla white, ca. 1.75 mm. long, tubular, slightly narrowed at the throat, glabrous, tube 1 mm. long, lobes 0.75 mm. long and broad, ovate, patent. Anthers 0.8 mm. long, 0.3 mm. broad at base, gradually narrowed towards the acutish apices, sessile, inserted ca. 0.2–0.3 mm. above the corolla base. Style absent; stigma 0.5 mm. long, 0.5 mm. in diameter at base, conical, glabrous. Fruits 2 mm. high, slightly broader in diameter, globose, lobed; nutlets 4, glabrous, brown or pale brown, rugulose.

DISTRIBUTION: America, Europe, Africa, West Pakistan, India, East Pakistan, and Australia.

West Pakistan: GURJAT DIST.: Daffar, Pabia (?), *Jan Mohammad 44* (KAU). JHELUM DIST.: Salt Range, Daryala Jalep, — 500 m. *Siddiqui 3662* (RAW, BM). KARACHI DIST.: Karachi, *Kazmi s.n.* (PES); *Jafri s.n.* (E); *Nath* in *R. R. Stewart 13120a* (GH); Karachi, Korangi, *Jafri 1452* (E); Malir, *Nath* in *R. R. Stewart 16590* (GH); *Kazmi s.n.* (PES); Malir, Memon Goth, *Tasnif s.n.* (KAU); Drigh Road, *Rahman Beg* in *R. R. Stewart 25723* (MICH); Band Murad Khan, *Tasnif & Aziz 816* (PES); Clifton, in stony and waste places, *Herb. No. 3410* (LAH); *Kazmi s.n.* (PES). LAHORE DIST.: near Shahadra river bank, *Shafi 8268* (LAH). PESHAWAR DIST.: Peshawar-Charsadda Road, at about 8 miles from Peshawar, on both sides of river, flowers white, *Burtt 974, 570* (E).

Heliotropium curassavicum is the only halophytic species of the genus with glabrous leaves and glabrous and hollow stems found in West Pakistan.

24. **H. supinum** L. Sp. Pl. 130. 1753; DC. Prodr. **9**: 533. 1845; Boiss. Fl. Orient. **4**: 127. 1875; C. B. Clarke in Hook. f. Fl. India **4**: 149. 1883; Cooke, Fl. Bombay Presidency **2**: 209. 1908; Riedl in Rechinger, Fl. Iranica **48**: 52. 1967.

Lithospermum heliotropoides Forssk. Fl. Aegypt.-Arab. 39. 1775.
Piptoclaina supine G. Don, Gen. Syst. **4**: 364. 1838.
P. malabarica G. Don, *Ibid.*
H. coromandelianum Retz. Obs. Bot. **2**: 9. 1781.
H. malabaricum Retz. *op. cit.* **4**: 24. 1786.
H. supinum var. malabarica (Retz.) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 149. 1883.

TYPE: "Habitat Salmanticae juxta agros Monspelii in litore" *Herb. No. 179.8* (LINN).

ICON.: Wight, Icones Pl. Indiae Orient. **4**: *t. 1387*. 1848.

Annual, prostrate, much branched, branches pale grayish to pale brown, up to 45 cm. long, densely clothed with soft trichomes 0.2–1 mm. long; short trichomes usually retrorse, appressed, the long ones spreading. Leaves petiolate, petioles of the lower leaves up to 3 cm. long, of the upper leaves shorter (a minimum of 3 mm. long), slender, villous; lamina ovate, obovate, ovate-lanceolate, or elliptic, usually subobtuse, rarely acute, margins entire, sometimes slightly revolute, nerves deeply sunken on the upper surface, not very prominent below, 1–2.5(–3) cm. long, 0.5–12 mm. broad; upper surface covered with white, silky, appressed trichomes intermixed with subappressed trichomes up to 1 mm. long, lower surface more densely hairy especially on nerves. Inflorescence much contracted when young, later elongated, usually 2–5(–8) cm. long, with uniseriate flowers, closely set when young, later up to 8 mm. apart. Calyx deciduous, 2–2.5 mm. long, at fruiting much enlarged and up to 5.5 mm. long, subsessile or at fruiting short pedicellate, pedicels up to 1 mm. long, divided 1/4–1/3 of their length, lobes ovate, obtuse, erect or suberect, 1 mm. long, densely covered with appressed and spreading hairs up to 1 mm. long, the divisions between the lobes marked down to the calyx tube by a thin easily tearable membrane. Corolla cylindrical, 2.5–3.5 mm. long, externally covered with short retrorse hairs, glabrous within, lobes rounded, patent, 0.5 mm. long and broad. Anthers 1 mm. long, 0.5 mm. broad at the roundish or ± truncate base, gradually narrowed towards the acute apex, sessile, inserted about 1 mm. above the corolla base. Stigma conical-elongate, with a prominent stigmatic ring, apex hirsute, 0.5–0.6 mm. long; style ± equalling the stigma, glabrous. Fruits of usually one developed nutlet or sometimes with 1–2 or rarely 3 abortive ones; nutlets dark brown, rounded and obscurely tuberculate on the back, usually with strong light brown margins.

DISTRIBUTION: South Europe, North Africa, Arabia, Syria, Iraq, West Pakistan, India, and introduced in South Africa and Australia.

West Pakistan: DADU DIST.: Karachi to Dadu, between Amri and Laki, shaded tamarisk woodland, *Kazmi 2463* (PES); *Lamond 833* (E); *Rechinger 28680* (G, W). HYDERABAD DIST.: Hyderabad University Campus, *Kazmi s.n.* (PES). MIRPUR KHAS DIST.: Gadro, *Zaman & Hussain s.n.* (PFI–M). Miscellaneous: northwest India, *Royle s.n.* (K).

5. **Sericostoma** Stocks ex Wight, Icones Pl. Indiae Orient. **4**(*2*): 15. *t. 1377*. 1848.

TYPE SPECIES: *S. pauciflorum* Stocks ex Wight.

Small strigose branched shrub. Leaves alternate. Flowers small, axillary, sessile, solitary, or the upper in a bracteate raceme. Sepals 5, narrow. Corolla tube short, mouth wide, closed with hairs; lobes 5, imbricate in bud, obtuse, spreading. Stamens 5, subincluded; anthers oblong, obtuse. Ovary deeply 4-lobed; style short; stigma subcapitate. Nutlets 4, ovoid, substipitate, scar basal; receptacle flat.

A monotypic genus restricted to West Pakistan and adjoining West India.

S. pauciflorum Stocks ex Wight, Icones Pl. Indiae Orient. **4**(*2*): 15. *t. 1377*. 1848; Hook. Icon. **9**: *t. 804*. 1852; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 175. 1883; Cooke, Fl. Bombay Presidency **2**: 220. 1908; Riedl in Rechinger, Fl. Iranica **48**: 54. 1967.

TYPE: Scinde: Baikur prope Deesa, *Stocks s.n.* (K-holotype; GH, W-isotypes).

Small perennial, woody at the base, branched, erect or suberect shrub, 10–50 cm. tall; herbaceous stem and branches covered with loose, short, appressed trichomes, usually deciduous with age. Leaves linear, lanceolate or oblong-ovate, 5–35 mm. long, 2–5(–10) mm. broad; nerves and veins inconspicuous on the upper surface, slightly raised below, both surfaces uniformly and loosely covered with short appressed trichomes arising from tuberculate bases in the older leaves; margins entire, apices subacute to obtuse. Inflorescence terminal rarely axillary, short, usually 2–6-flowered, becoming loose and longer with age, up to 10 mm. long, bracteate, bracts much reduced, 1–2 mm. long. Calyx deciduous at maturity, subsessile, 2.5–3 mm. long, slightly enlarged at fruiting, deeply divided, lobes lanceolate, acute, subequal, ± imbricate, hairy. Corolla 3–3.5 mm. long, up to 5 mm. in diameter, lobes 2 mm. long, 1.5 mm. broad at base, rounded to ovate, spreading and recurved, throat densely hairy, annulus represented by a narrow band of trichomes just above the base of corolla tube. Filaments equal, 0.8–1.1 mm. long, affixed at the summit of the corolla throat directly beneath the base of the corolla sinuses; anthers slightly longer than filaments, exserted. Style 1–1.3 mm. long, shorter than the nutlets; stigma terminal. Gynobase plane or even depressed at the center. Nutlets with a short downwardly directed stipe bearing the attachment at its lower end, ovoid-oblong, 2–2.5 mm. long, 1.5 mm. broad, slightly tuberculate, brownish.

DISTRIBUTION: West Pakistan, India.

West Pakistan: KARACHI DIST.: Between Hawkes Bay and Bungalow village. *Kazmi 864* (PES); inter Damloti et Khadiji, in arenosis, *Rechinger 28499, 28501, 28515* (G, W); Cape Monze, *Rechinger 27516* (W); Sonmiani, *Rechinger 27545,*

27546 (W); Hab Cauki, *Rechinger 28585* (W). Miscellaneous: Nagar Parker, *G. Popov 349* (BM); Baikur prope Deesa, *Stocks s.n.* (GH, K, W).

The leaves of *Sericostoma pauciflorum* vary from very short linear to broadly ovate-oblong, up to 3.5 cm. long, but this variation cannot be correlated with any character of the floral parts or any geographical area in its distribution.

6. **Bothriospermum** Bunge, Enum. Pl. Chin. Bor. 47. 1832.

TYPE SPECIES: *B. chinense* Bunge.

Weak annual or biennial herbs. Leaves alternate, ovate to lanceolate. Flowers small, blue or white, axillary, pedicellate, the upper going off into a bracteate raceme. Calyx 5-partite, lobes free at the base, narrow, not or slightly enlarged in fruit. Corolla tube short, cylindrical, throat with 5 scales, lobes imbricate in bud, later spreading. Stamens 5, included; anthers ovate, obtuse. Ovary deeply 4-lobed; style short; stigma capitate. Nutlets 4, ellipsoid, granular-scabrid, inverted, parallel, their backs proximate with a double bony margin, tumid and inconspicuous, with a small apical or subapical attachment.

Species 3 to 4, all of them occurring in China and one extending up to Japan in the east, and Afghanistan, Pakistan, and India in the southwest.

B. tenellum (Hornem.) Fisch. & Mey. Index Sem. Hort. Petrop. 1: 23. 1855; DC. Prodr. 10: 116. 1846; C. B. Clarke in Hook. f. Fl. Brit. India 4: 167. 1883; Kashyap, Lahore Dist. Fl. 171. 1936; Riedl in Rechinger, Fl. Iranica 48: 56. 1967.

Anchesta tenella Hornem. Hort. Hafn. 1: 176. 1815.
Cynoglossum diffusum Roxb. Fl. Indica ed. Wall. 1: 7. 1824.
C. prostratum D. Don, Fl. Nepal. 100. 1825.

TYPE: "Hab. in China" in Herb. Vahl (as *Anchusa zeylanica*).

Prostrate, much branched at base, branches slender, simple or slightly branched, 8–25 cm. long; stem and branches covered with short appressed trichomes. Basal leaves obovate, lower cauline leaves petiolate, obovate-lanceolate to lanceolate, upper lanceolate, sessile, all between 15–30 mm. long, 3–8 mm. broad; margins undulate, apices acute; uppermost leaves bract-like, 7–8 mm. long, ± 2 mm. broad. Flowers pedicellate, pedicels 3–4(–5) mm. long, axillary, the upper going off into axillary racemes. Calyx ± 2 mm. long, divided to the base, lobes linear-lanceolate. Corolla ± 2.5 mm. long, tube equalling the calyx, lobes rounded, ± patent, throat with 5 trapeziform scales, emarginate at the apices. Anthers ovate, obtuse, included. Stigma capitate; style short. Nutlets ±1 mm. long, ellipsoid, granular-scabrid, inverted, parallel, their backs proximate with a double bony margin, tumid and inconspicuous, with a small apical or subapical attachment.

DISTRIBUTION: Afghanistan, Pakistan, India, China, Manchuria, Japan, Philippines, Mascarene and Hawaiian Islands.

West Pakistan: LAHORE DIST.: Lahore, *Sahai s.n.* (K). Miscellaneous: Where Chumuck joins the Jhelum, *Aitchison 364* (K).

7. **Echiochilon** Desf. Fl. Atlant. 1: 166. 1798.

TYPE SPECIES: *E. fruticosum* Desf.

Usually perennial plants. Inflorescence with numerous flowers, usually elongating and becoming unilaterally racemose. Calyx persistent, divided nearly to the base, lobes valvate or at least not evidently imbricate. Corolla small to large, radially symmetric to strongly zygomorphic, corolla lobes shorter than the tubular portion. Filaments deeply affixed in the corolla throat. Stigma subterminal always surpassed by the protracted sterile tip of the style. Gynobase elevated, attenuate, usually narrowly pyramidal and more than half the length of the nutlets. Nutlets with a prolonged sessile lateral attachment.

Species 17, distributed in North Africa, Arabia, Iran, and Pakistan.

E. persicum (Burm. f.) I. M. Johnston, Jour. Arnold Arb. **38**: 288. 1957; Riedl in Rechinger, Fl. Iranica **48**: 58. 1967.

Heliotropium fruticosum L. var. *persicum* Burm. f. Fl. Indica 41. *t. 19. fig. 1.* 1768.
H. persicum (Burm. f.) Lam. Encycl. Méth. Bot. **3**: 94. 1789.
Lithospermum kotschyi Boiss. & Hohen. var. *brevifolium* Bornm. Mitt. Thür. Bot. Ver. **6**: 59. 1894.
L. persicum Gaud. Bull. Soc. Bot. Fr. **65**: 62. 1918.
Sericostoma persicum (Burm. f.) B. L. Burtt, Kew Bull. **1949**: 138. 1949.

TYPE: Persia, *Burmann f. s.n.* (G-DC).

ICON.: Burm. f. l. c. *t. 19. fig. 1.* 1768 (as *Heliotropium fruticosum* var. *persicum*).

Decumbent shrub, old stems becoming woody, up to 8 mm. thick, usually branched above the middle, branches 5–15 cm. long, covered with straight, appressed trichomes 0.5–1 mm. long. Leaves usually ascending, oblong or oblong-lanceolate, thickish, 3–15 mm. long, 1–3 mm. broad, weakly conduplicate or the upper surface merely somewhat concave, lower surface convex, not costate; lowest 2–3 pairs of leaves on the shoot opposite, others alternate. Inflorescence racemose, unilateral, 3–8 cm. long, 10–20-flowered, terminating the leafy shoots and their branches, bracteate, bracts oblong, shorter than the calyx. Calyx at flowering 3.5–4 mm. long, lobes 2.5–3 mm. long. Corolla 4.5–6 mm. long, tubular-funnelformed, abaxial side 1–1.5 mm. shorter than the adaxial side, outer surface minutely villulose, lobes ascending, 1–1.5 mm. in diameter, margins crisped, throat bearing abundant yellow hairs inside, annulus usually marked only by an indistinct band of minute hairs about 0.5 mm. above the corolla base. Anthers 1.2–1.7 mm.

long, usually included; filaments 0.5–0.8 mm. long, unequal, borne at unequal heights, 2.3–3 mm. above the corolla base. Style 0.9–1.5 mm. long; stigma very short, low convex. Gynobase 1.5 mm. tall, abruptly narrowed above the broad base, base about 1 mm. broad. Nutlets 2–2.3 mm. long, above the base 1.5–1.7 mm. broad, gray or pinkish, usually one or more aborted, back convex, obscurely roughened or with a few scattered prominent tubercles; areola green, vertical or rarely somewhat oblique, abruptly contracted into a narrow groove extending upwards to above the middle of the nutlet.

DISTRIBUTION: Coastal areas of southern Iran and West Pakistan.

West Pakistan: Sind: Hala Range, *Vicary s.n.* (K).

The species most closely related to *Echiochilon persicum* appears to be *E. kotschyi* of the Islands of the Persian Gulf. The insular species, however, is very distinct, differing from *E. persicum* in its practically smooth nutlets, few-flowered inflorescence, small recurved leaves, and in its regular rather than zygomorphic corollas.

[*To be continued*]

THE GENERA OF THE CANNABACEAE IN THE SOUTHEASTERN UNITED STATES [1]

NORTON G. MILLER

CANNABACEAE Endlicher, Gen. Pl. 286. 1837, "Cannabineae," nom. cons.[2]

(HEMP FAMILY)

Rough, mostly aromatic, annual or perennial herbs; stems erect, scandent, or, in perennials, a subterranean rhizome bearing aërial branches, generally ridged or furrowed and either scabrous with long hairs or armed with sharp, rigid, medifixed trichomes often set on multicellular pedestals. Leaves palmately compound or lobed, sometimes simple, petiolate, serrate, generally decussate, but often alternate near the stem apex; lower (abaxial) leaf and leaflet surfaces sparsely or densely covered with hairs and glandular dots, upper (adaxial) surfaces usually crowded with cystoliths and rigid conic hairs with forward-pointing apices; stipules triangular, sometimes fused laterally, persistent. Plants dioecious, rarely monoecious, vegetatively dimorphic or not. Staminate inflorescences loose, erect or ± pendent, axillary, bracteate cymose panicles (thyrses). Staminate flowers small, pedicellate, regular, gynoecium completely absent. Perianth

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). The present treatment follows the plan initiated in the first contribution of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area dealt with includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. References followed by an asterisk are those which I have not been able to check.

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[2] Although the orthography of this family name has been disputed, and the spellings Cannabinaceae and Cannabiaceae were frequently used in the past, correctly formed, the name is derived from the stem of *Cannabis, Cannab-*, plus the ending *-aceae*. A recent proposal (Taxon **15**: 211, 212. 1966) to change Cannabaceae to Cannabinaceae (and to modify certain others in the list of conserved family names found in Appendix II of the current edition of the International Code of Botanical Nomenclature) was rejected by ballot during the nomenclature sessions of the XI International Botanical Congress, Seattle, 1969.

uniseriate; tepals 5, greenish or whitish, rarely otherwise, boat-shaped, downy, sometimes glandular. Stamens 5, erect in bud, hypogynous, opposite the perianth segments; anther walls thin, dehiscence longitudinal, basipetal; filaments short, weak; pollen suboblate, triporate, with the tectum thickened around the pores, surface finely granular, ca. 25 μ in diameter. Carpellate inflorescences axillary, basically cymose, spicate, various types of glandular hairs usually present. Carpellate flowers often paired, subsessile, tightly covered or loosely subtended by a bract or bracteole. Perianth uniseriate, thin, undivided, unlobed, at maturity tightly covering nearly the entire ovary. Gynoecium basically bicarpellate, reduced androecium not apparent; style short, apical, central, divided into 2 long filiform stigmatic branches densely covered with soft hairs and caducous soon after pollination; ovary superior, 1-locular with 1 bitegmic anatropous, crassinucellar ovule pendent from near the apex of the locule, the micropyle formed from the inner integument. Fruit a crustaceous achene, covered either loosely or tightly by the perianth. Seed 1; seed coats 2, membranaceous, green; endosperm sparse, fleshy; embryo curved or spirally coiled. Embryo sac development of the Polygonum type, embryogeny of the Onagrad type. TYPE GENUS: *Cannabis* L.

A small family of two genera with several economically important species, native entirely to parts of the temperate Northern Hemisphere, but now widespread throughout the world, although less frequent in tropical regions. *Cannabis* and *Humulus* form a natural unit. They have many characters in common, including a basic similarity in floral morphology, anatomy, and vesture.

A variety of trichome types occurs on members of the family. Nonglandular hairs are mostly unicellular, rarely uniseriate, often with silicified walls, and of three kinds: (1) short, conic hairs with expanded bases that penetrate the leaf mesophyll and frequently contain a single large cystolith of calcium carbonate, occurring on adaxial surfaces, (2) unicellular two-armed hairs on petioles and young axes, and (3) long, lax hairs mostly on abaxial leaf surfaces and stems. Glandular hairs include the following types: (1) unicellular-stalked discoid glands found mostly on abaxial leaf surfaces, bracts, and axes, (2) capitate glands supported by uniseriate or biseriate stalks, most common in the carpellate inflorescence of *Cannabis sativa*, and (3) short-stalked glands with cup-shaped heads, restricted to the carpellate inflorescence of *Humulus Lupulus*.

Species of *Cannabis* and *Humulus* are wind-pollinated. Stigmata have been reported to be exserted from the bracts and receptive 4–5 days before pollen is shed from nearby staminate plants. Staminate flowers are generally pendent at anthesis, but rather than expelling their pollen at once, the anther sacs gradually dehisce basipetally by a longitudinal slit. Initially, pollen sifts through an apical oval opening having the appearance of a pore. A single inflorescence of *Cannabis sativa* has been estimated to produce more than 500 million pollen grains. Dispersal of *Humulus Lupulus* is reported to be facilitated by the adherence of the wing-like

bracteole to the achene. At places in the midwestern United States *Cannabis sativa* achenes have been found in the crops of mourning doves, which may have an active role in the local dispersal of this species.

The Cannabaceae appear to be closely related to both the Urticaceae and Moraceae, with which they share a number of characters. These families may have been derived from the Magnoliales through the Hamamelidales (Cronquist, Takhtajan, Tippo). A relationship with the Malvales, among others, has also been suggested (Thorne and others).

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KEY TO THE GENERA OF THE CANNABACEAE

General characteristics: *erect or scandent herbs, scabrous or armed with rigid climbing hairs, and often with glandular trichomes; leaves palmately compound or lobed, sometimes simple; staminate inflorescence a loose cymose panicle, staminate flowers with 5 free tepals and 5 antitepalous stamens; carpellate inflorescence spicate, carpellate flowers small, perianth uniseriate, continuous, tightly appressed to the ovary, ovary 1, superior, 1-locular, with a single ovule pendent from near the apex of the locule, style branches 2, filiform; fruit an achene covered by the persistent perianth.*

A. Plants erect herbs; leaves palmately divided into long, lanceolate, serrate leaflets; variously provided with trichomes, but two-armed hairs absent from stems or branches and petioles; carpellate inflorescences erect; gynoecium tightly ensheathed by a beaked persistent bracteole with long-stalked glandular hairs. ..... 1. *Cannabis*.

A. Plants scandent herbs; leaves palmately lobed or simple; two-armed hairs present on stems and petioles; carpellate inflorescences pendent; gynoecium loosely subtended by a bracteole with short-stalked and cupulate or sessile glandular hairs. ..... 2. *Humulus*.

1. **Cannabis** Linnaeus, Sp. Pl. 2: 1027. 1753; Gen. Pl. ed. 5. 453. 1754.

Tall (to 5 m.), erect, branched or unbranched, coarse, tap-rooted, weedy annual herbs occurring in waste places, disturbed ground, and alluvial flats; stems obtusely polygonal or round in cross section, ± ribbed or furrowed, often hollow at maturity, scabrous and sparsely covered with resinous dots, especially on the young parts of the axis. Leaves decussate near the base, alternate toward the apex and on branches, palmately compound with 3–15 (usually 5–9) coarsely serrate, long, lanceolate leaflets; the lower surface whitish green, with widely spaced yellow to brownish resinous dots and strigose hairs, the upper surface darker green with large, stiff, bulbous-based conic trichomes; stipules narrowly triangular. Plants dioecious, rarely monoecious except in certain cultivated strains and experimental plants; dimorphic, staminate plants tall, slender, with few leaves in the terminal inflorescence, dying soon after flowering; car-

pellate plants stocky, with a dense crown of leaves associated with the inflorescence, living for several months after pollination. Staminate inflorescences loose cymose panicles, long, if originating from the axils of foliage leaves, short, if from the axils of stipules. Staminate flowers pedicellate, small, pendent at maturity, caducous soon after shedding pollen. Tepals greenish, rarely purplish, quincuncial in bud and widespread at anthesis. Anther walls thin, bearing glandular hairs at the junctures of anther lobes; pollen sacs 4 (bilocular at anthesis); filaments flaccid. Carpellate inflorescences congested series of axillary false spikes; the main axis, leaves, petioles and bracts associated with carpellate inflorescence often densely covered with resinous capitate or ± sessile glandular hairs. Carpellate flowers sessile or nearly so, ensheathed by a glandular, beaked perigynal bracteole and subtended by a bract (stipule?). Perianth papery, continuous, closely appressed to the ovary. Fruit an ovoid, somewhat compressed achene with the perianth persistent, reticulate, and often mottled with brown; pericarp 5 layered, the inner palisade layer the thickest. Seed 1, ovoid; perisperm 1 cell-layer in thickness; endosperm fleshy, with a chalazal haustorium; embryo curved, U-shaped, flexed in the region of the epicotyl, with the radicle and cotyledon tips pointing toward the micropylar end of the seed (ovary apex); $2n = 18 + XX$ or XY. TYPE SPECIES: *C. sativa* L. (Ancient Greek and Latin name for hemp, said to come from Arabic, *kinnab*, or Persian, *kannab*.) — HEMP, MARIJUANA.

A genus of one (or perhaps more) species, originally indigenous to temperate parts of Asia, probably to the desert region immediately to the south and east of the Caspian Sea, but now occurring as an adventive or naturalized weed throughout most of the world. *Cannabis sativa*, a decided nitrophile that grows well in close association with man and his wastes, is widespread in the United States and most frequently collected in Kansas, Nebraska, Iowa, and Illinois. It is known from only a few stations in the Southeast but may be more abundant than herbarium specimens and literature reports imply.[3] *Cannabis ruderalis* Janisch. (Učen. Zap. Gos. Saratov. Univ. 2(2): 14. 1924), a possible second species occurring in Central Asia, southeastern Russia, and as a weed in eastern and Central Europe, is reported to differ from *C. sativa* in size and achene characters. Most authors accept only one species, and whether the diagnostic characters of *C. ruderalis* are distinct and do not overlap the extensive variability of *C. sativa* remains to be worked out carefully.

Cannabis sativa has been much used as an experimental plant. Interest was focused early on monoecious hemp plants and the "reversion" of carpellate plants to staminate ones and vice versa. For example, seeds planted in summer at Columbus, Ohio, yielded about equal numbers of carpellate and staminate plants, but seeds from the same lot sown indoors

[3] Haney and Bazzaz plausibly relate the apparent rarity of *Cannabis sativa* in the southeastern United States to derivation of naturalized hemp in North America mostly from temperate European and Chinese fiber strains which are ill adapted to growing under environmental conditions present in the Southeastern States.

in December, gave a crop in which more than three-quarters of the carpellate plants produced intersex or pure male flowers and a similar proportion of the staminate plants occurred with intersex or pure female flowers. After the discovery of photoperiodic responses in plants about 1920, it was realized that hemp was a short-day plant in which sex reversal was correlated with exposure to ever shorter periods of light. Other factors, including temperature and available soil nutrients, apparently also exert some control. However, the genetic basis of sexuality in hemp is still not fully understood. Although environment was originally considered to have the major role and Mendelian inheritance to be inconsequential, different workers have demonstrated the presence of a heteromorphic chromosome pair in staminate meiotic material from several dioecious strains. A heteromorphic pair has been less convincingly shown in certain monoecious strains. In dioecious hemp, sex determination is thought to be under an XX = ♀ and XY = ♂ system, and derived monoecism has been explained in two ways: monoecious plants are all XX, and variation in sex expression is due to heterozygous genes on the X-chromosomes and autosomes; or XX, XY, and YY monoecious plants can occur, but only autosomes determine sex. Unfortunately, somatic karyotypes have been imperfectly investigated.

The morphology of the spicate carpellate inflorescence of hemp has been interpreted in several ways. Buds are reported to occur in the axils of both stipules and leaves, and, according to Camp (1932), stipular buds (two at each node) give rise to short determinate branches bearing single flowers, whereas the true axillary bud produces an indeterminate branch bearing leaves and stipular flowers but no secondary axillary branches. Bud primordia are visible in the axils of reduced leaves borne on the axillary branch, but suppression is broken only under extraordinary conditions. In an alternate interpretation (see Hayward, 1938) a pair of flowers, each subtended by a stipule, is claimed to arise in a leaf axil. A secondary branch, also issuing from the leaf axil, bears another leaf with stipules and flowers, and this, in turn, produces an axillary branch of the third order. The staminate inflorescence is composed of a main indeterminate axis bearing secondary branches from both the axillary and stipular buds near the base, but only from the stipular buds toward the apex (Camp, 1932). The staminate inflorescence of hemp is called a panicle or raceme by most authors, but the side branches are clearly cymose.

Zander has studied the poorly differentiated, unbranched, and inarticulate laticifers that occur in the stem of hemp. He concludes that "the anatomical behavior and developmental history of hemp laticifers are different in comparison with the rest of Moraceae" (transl.).

Three economically important products are obtained from *Cannabis sativa*. Perhaps least significant (except in Russia) is a drying oil pressed from the fruits. The oil is used as a substitute for linseed oil in paints and varnishes and occasionally in soap making. After expressing, the "seed"-cake may be fed to cattle. In parts of eastern Europe and Russia roasted hemp "seeds" are eaten by humans, and in the United States *Cannabis*

achenes are sold in seed mixtures prepared for cage-birds and outdoor bird-feeders. At one time uneaten achenes from such mixtures were a major source of spontaneous hemp plants, but now the "seeds" are sold only after the embryos have been killed.

In many parts of the world hemp is grown on a commercial basis for fibers which are made into ropes, twines, bags, and webbing. Clothing was once made from the finer grades, and the strong, durable fibers of hemp were used extensively for sail cloth. A tarred caulking material, oakum, is produced from shorter fibers and tow. Hemp is most successfully grown for fibers on rich, humified loam in a mild, humid climate. Individual fibers are about a centimeter long and occur in two zones in the stem. The outer, primary fibers are longer and thicker walled than the inner, secondary fibers, and both series are separated by several layers of parenchyma, a feature that enables the isolation of the primary fiber-bundles by retting. In general, internode and fiber-bundle length are in direct proportion, and tall cultivars with fewer nodes are sought. Staminate plants produce the finest grade of fibers. Because staminate plants die soon after shedding pollen, while carpellate plants live until the fruits mature, breeding programs have been directed toward producing either monoecious strains with the tall growth-habit of the staminate plant or uniform-ripening dioecious races. Colchicine-induced tetraploid strains, which give a greater yield of higher quality fiber than normal diploids, are grown to some extent. Hemp agriculture in the United States first started on a limited basis in New England, in 1632, with seeds brought to the Colonies from England. In the 1800's, particularly during the midcentury years, hemp was extensively grown in the Bluegrass Region of Kentucky from seeds of Chinese origin. During the 1850's, 75,000 tons were harvested annually in the United States, but production had dropped to 5000 tons or less by the early 1900's. Acreage in hemp dramatically increased during both World Wars. In 1943, as a response to the inaccessibility of Manila hemp, nearly 63,000 tons were produced. All hemp fiber used in the United States in recent years has been imported, generally from European sources.

The hemp plant is the source of an important narcotic drug. Its effect on humans, although at present mostly lacking scientific documentation, seems to be to induce a general state of euphoria, frequently broken with periods of depression, and often accompanied by vivid mental imagery. The drug is apparently widely used throughout the World, in spite of severe penalties. There is some evidence that the use of hemp drugs in the United States started about 1910 in New Orleans. The narcotic principle occurs in the resinous material that accumulates most abundantly on tissues of the carpellate inflorescence. Among the numerous compounds isolated from the resin in recent years, the dibenz-α-pyrans, Δ^{1}- and Δ^{16}-*trans*tetrahydrocannabinol (THC), have been found to be the major agents of intoxication in man. At present, tetrahydrocannabinols are reported from no other plant.

Methods of taking the drug vary somewhat from culture to culture.

In the United States, *marijuana* is a mixture of the resin and various plant fragments, generally from the carpellate inflorescence, while *hashish* is a term restricted to the pure resin. Both forms are most often smoked. In India the resin may be eaten or drunk in various carriers, especially milk. The word *assassin*, taken directly from the Arabic *hashshāshīn*, *hemp eaters*, entered the English language at the time of the Crusades. The hashshashins were a group of murderers who were supposed, perhaps erroneously, to have carried out their missions, while intoxicated by hashish.

The largest amount of resin is produced by flowering carpellate plants in hot, dry climates. An increase in humidity lowers production, and stems, lower leaves, and seeds contain the least amount of resin. Plants grown in India have been reported to contain 20 per cent resin, those from Mexico 15 per cent, and samples from Kentucky and Wisconsin 8 and 6 per cent, respectively. There are conflicting statements in the literature about the occurrence of THC in carpellate and staminate plants of different geographic origin and in strains grown for fibers and oil. Selection of high-yield fiber or oil cultivars apparently may result in a loss of THC, in spite of the retention of high resin-production. Staminate plants from certain strains lack THC, but the intoxicating principle may occur in male plants of other cultivars. To date, a thorough analysis of the resin from wild self-seeding types and cultivated dioecious and monoecious strains grown in various parts of the World for fiber, oil, or the drug has not been made. Gas chromatographic methods would be useful in such a study.

Forensic identification of marijuana is based on microscopic examination of the sample, in conjunction with one or several chemical tests applied to a petroleum-ether extract of the resin. The glandular and nonglandular hairs occurring on the upper and lower leaf surfaces, petioles, and bracts of the inflorescences of both sexes are considered distinctive, especially when compared with an authenticated specimen. Since the cystoliths of *Cannabis sativa* are composed of calcium carbonate, addition of dilute hydrochloric acid will cause a slight effervescence, which is visible through a low-power microscope.

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2. **Humulus** Linnaeus, Sp. Pl. 2: 1028. 1753; Gen. Pl. ed. 5. 453. 1754.

Rough, scandent and dextrorse-twining annual or perennial herbs of river and stream bottoms, thickets, hedgerows, roadsides, and other disturbed sites; with long taproots, or, if perennial, with a massive rhizome and abundant adventitious roots; aërial stems weakly ridged, often hexagonal in cross section, rigid two-armed climbing hairs frequent near the apex and often on multicellular emergences; axillary branches mostly from upper nodes. Leaves generally decussate, or alternate when associated with an inflorescence, sometimes simple and cordate but more often palmately lobed, serrate; venation strictly palmate; petioles with two-armed trichomes; lower leaf surfaces with clear or yellowish resinous dots and widely spaced hairs on lamina and major veins, upper surfaces densely covered with cystoliths and short, rigid conic hairs; stipules lanceolate, two per petiole or coalesced laterally into one. Plants dioecious, rarely monoecious when growing in nature. Staminate inflorescences axillary, sometimes terminal, erect or ± pendent, many flowered, loose cymose panicles. Staminate flowers pedicellate, small. Tepals greenish, bearing on the abaxial surface glandular dots and occasionally long, rigid trichomes. Glandular dots at junctures of the anther lobes either present or absent. Carpellate inflorescence spicate, consisting of a series of ovate or acuminate stipular bracts and bracteoles subtending solitary or paired flowers; bracts and bracteoles pubescent or ciliate, with sessile glandular dots or short-stalked cupulate lupulin glands on abaxial surfaces. Carpellate flowers with short pedicels, borne in the axil of a bracteole which at maturity is large and either brown and membranaceous or ± foliar and green, sometimes reddish pigmented. Perianth continuous, thin, appressed to the ovary, either covered with lupulin glands or not. Fruit a lenticular or ± round achene, tightly or loosely ensheathed by the brownish or sometimes mottled persistent perianth; pericarp crustaceous. Seed 1; embryo coiled into a tight spiral, cotyledons long, radicle pointing toward the micropyle. Type species: *H. Lupulus* L. (Late Latin name for this plant, from Old Slavic.) — HOP.

A genus of two species native to portions of the North Temperate Zone but now widely cultivated, escaped, or naturalized throughout temperate areas of both hemispheres. Originally indigenous to eastern Asia (China, Taiwan, Manchuria, Korea, and Japan), *Humulus japonicus* Sieb. & Zucc.[4] is naturalized in eastern North America southward to North Carolina, South Carolina, and Tennessee. It differs from *H. Lupulus* L. in many characters, among which the occurrence of ciliate hairs on the margins of the bracteoles and stipular bracts, the absence of lupulin glands, and the presence of from 5 to 7 leaf lobes (*vs.* 0–3 [5] in *H. Lupulus*) are the most readily observed. Wild *H. Lupulus* is disjunct in the Northern Hemisphere. It occurs in Japan, a part of North America, and from central Asia to southern Europe, a range that appears to fit one of the Arcto-Tertiary distribution patterns. The populations in each region have been considered distinct species, although recent work indicates that only subspecific differences exist between them. *Humulus Lupulus* presently is found throughout most of the United States and southern Canada, but the actual range of the native North American hop, which Nuttall, in 1848, named *H. americanus* (based on a Gambel collection from New Mexico), remains unknown. The early introduction of *H. Lupulus* from Europe for use in brewing and its subsequent escape and spread have made it difficult to decide whether a particular plant is native or introduced. However, pollen of *H. Lupulus* has been found at several sites in the upper Midwest in lake sediments deposited long before the presence of European man in the New World. Future detailed analysis of postglacial sediments from elsewhere in North America could ultimately solve the problem of the pre-settlement distribution of the native hop on this continent.

The spicate carpellate inflorescence of *Humulus* consists of a condensed primary axis bearing reduced secondary branches (Ehara, 1955; Hamaguchi, 1955). Internodes, although shortened, are clearly discernible. In *H. Lupulus* two flower pairs normally occur per node, each pair being subtended by a bract and each individual flower by a bracteole. Peduncles and pedicels are short, and the flowers are subsessile. The nodal flower clusters are interpreted as cymes in which the third (first opening) flower of each pair and the flower or branch between the pair are suppressed. Infrequently a reduced leaf is found at certain nodes between the two enlarged bracts, indicating their homology with stipules. Stipular bracts generally have pointed apices, while bracteoles are obtuse. The

[4] Merrill (Trans. Am. Philos. Soc. **24**: 138. 1935) contends that *Antidesma scandens* Lour. (Fl. Cochinch. **2**: 617. 1790) is unmistakably the species widely known as *Humulus japonicus* Sieb. & Zucc. (Abh. Akad. Wiss. München **4**(3): 213. 1846; also issued with different pagination as Fl. Jap. Fam. Nat. **2**: 89. 1846). If Merrill is correct, his combination, *Humulus scandens* (Lour.) Merr., should be adopted. Unfortunately, Loureiro's description, based on only a staminate plant, is superficial and mentions glabrous leaves and unarmed stems, two characters that are difficult to attribute to *H. japonicus*. Further, since the specimen upon which Loureiro based his description apparently has not been preserved (see Merrill, *loc. cit.*), the applicability of the name *H. scandens* seems open to question.

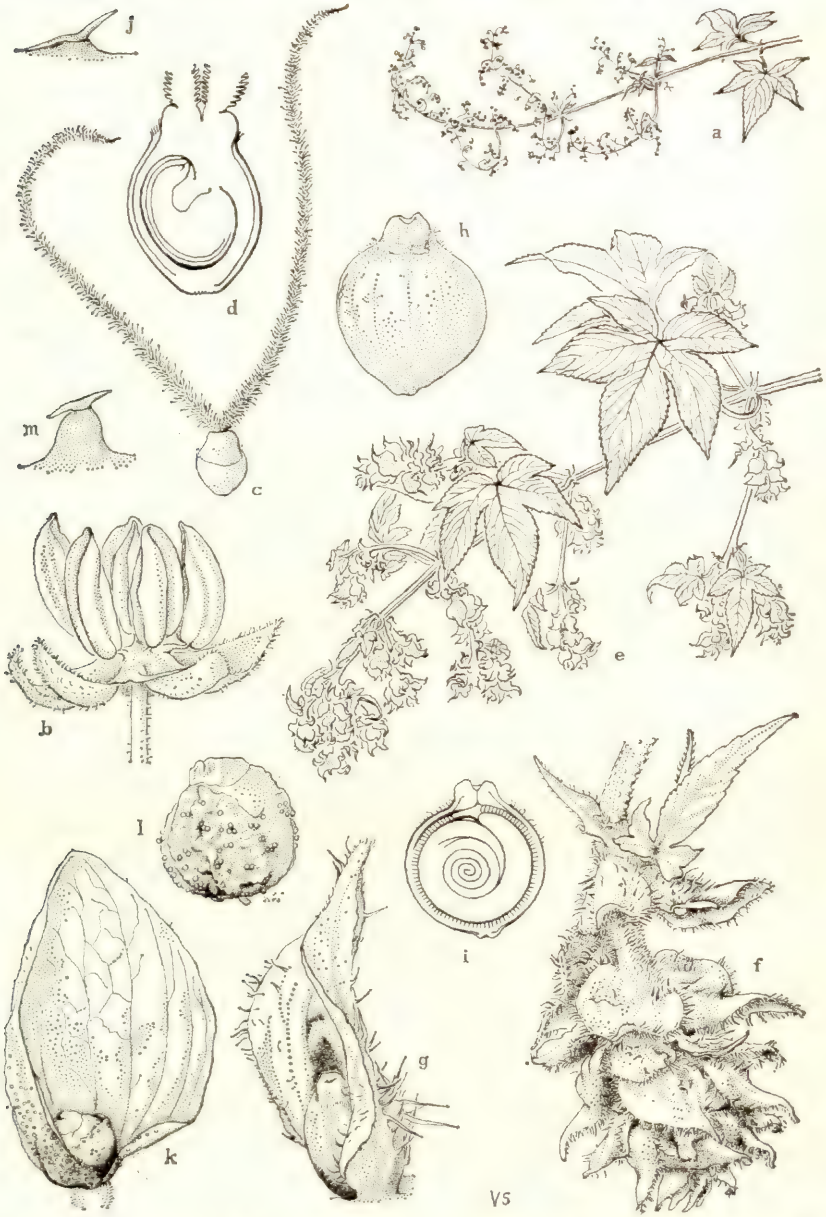

FIG. 1. **Humulus.** *H. japonicus*: a–j. a, terminal staminate inflorescence, × 1/4; b, staminate flower, × 10; c, carpellate flower with partly developed perianth, × 12; d, longitudinal section of ovary showing ovule, style branches mostly removed, × 20; e, terminal carpellate infructescence, × 1/2; f, fruiting spike showing pointed stipular bracts and bracteoles with blunter apices, × 2; g, nearly mature achene in axil of bracteole, × 5; h, mature achene with tightly appressed perianth, × 6; i, achene with embryo in diagrammatic longitudinal

carpellate spikes of *H. japonicus* and *H. Lupulus* are morphologically similar except that in the former only one flower (with its associated bracteole) occurs in the axil of a stipular bract. Sterile bracts are commonly present at the base of the inflorescence.

The diploid chromosome number in *Humulus Lupulus* is 20, and Winge in 1923 first demonstrated a heteromorphic pair of sex chromosomes (XY) in staminate plants of European origin (see Ono & Suzuki, 1962). Although carpellate plants of this species apparently uniformly have a homomorphic pair of sex chromosomes (XX), more recent research on the chromosomal makeup of staminate hop has shown considerable variability which seems to be correlated with the geographic origin of the plants. Working with the wild hop of Japan, Ono (1955, 1962) found that the sex chromosomes almost invariably took multiple forms consisting of four or six chromosomes. Both types, the more frequent tetravalent and the rarer hexavalent, presumably have arisen by reciprocal translocations between the original XY chromosome pair and certain autosomes. At meiosis, components of the sex chromosome complex conjugate end to end. Cytological studies on staminate European and American hops have been less extensive, but, in general, the simple XY type seems to prevail in plants from Europe, while in American samples homomorphic XY males, heteromorphic XY males (X length: Y length = 10:8 instead of 10:5 as in the European hop) and tetravalent complexes have been observed. Sex chromosomes have been found in *H. japonicus* also, but instead of an XY mechanism, the staminate plant has a $2n$ chromosomal complement of 14 autosomes and 3 sex chromosomes, Y_1XY_2. The Y chromosomes are heterochromatic for most of their length. During anaphase I of meiosis in staminate plants, 8 chromosomes go to one pole and 9 go to the other. Carpellate plants have a $2n$ number of 14 + XX.

Bracteoles, perianths, and, to a lesser degree, stipular bracts of the mature fruiting spike of *Humulus Lupulus* are covered with large cup-shaped glands filled with a yellow resinous substance, lupulin, that is used to impart flavor and aroma to beer. Bacteriostatic agents in lupulin also inhibit the growth of spoilage bacteria, while permitting yeast to develop freely and ferment the wort, a mixture of sugar (obtained by enzymatic conversion of starch from various grains) and water. Hops may be added to the wort while it is being boiled prior to the onset of fermentation or to the final beer in the storage tank. In the former case, the bittering substances are formed from the resin constituents during boiling, while in the latter the flavoring is derived from essential oils in the resin.

Lupulin is composed of soft and hard resins, but only components of the soft resin apparently contribute to a beer's flavor. The aroma of beer

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section, endocarp hatched, × 6; j, rigid 2-armed trichome from petiole, × 25. *H. Lupulus*: k–m. k, mature achene in axil of bracteole, × 4; l, mature achene with persistent ± inflated perianth and lupulin glands, × 10; m, rigid 2-armed trichome from petiole on multicellular pedestal, × 25.

derives solely from essential oils, a distinct group of compounds. Soft resin can be separated into α-acid, β-acid, and uncharacterized fractions, each category containing a number of distinct organic compounds. Isomerization of the α-acids during boiling yields water-soluble, bitter-tasting isohumulone and its analogues, which strongly inhibit the growth of Gram-positive bacteria. Lupulone in the β-acid fraction is also bacteriostatic. The percentage of cohumulone in the α-acid component has been shown to vary in amounts which correspond to groupings or morphological features recognized as characteristic of hops either native or long-cultivated in England, the European continent, and America (Davis & Burns, 1962).

The cultivated hop was introduced into North America in 1629, and by 1650 commercial crops were being harvested in Virginia and New Netherlands. During the 1800's and early 1900's New York was an important region of hop cultivation, although following the Civil War, the industry began to spread westward through Pennsylvania to Wisconsin. In the United States today the leading areas of hop production are Idaho, Washington, Oregon, and California, where three principal varieties are grown. The first, the English hop, was obtained by crossing a wild carpellate plant from Manitoba with an English staminate plant, and the second, the Fuggle hop, was selected from seedlings raised in England. The origin of the third, Cluster hops, is less certain. The Late Cluster type originated during Colonial times on the eastern seaboard, perhaps as a seedling from an English variety then in cultivation, while the Early Cluster type was derived as a bud sport directly from the Late Cluster hop. At the present time the most widely grown hops in the United States are the Cluster varieties. Hops are also cultivated in Canada, Europe, northern India, China, Manchuria, Japan, South Africa, southeastern Australia and Tasmania, New Zealand, and southern South America. Pollination is not necessary for the development of the spike and lupulin glands, so staminate plants are rarely raised in hop yards, except for breeding purposes. Rhizome cuttings are used for propagation.

Hops require a well-drained, nitrogen-rich soil and will not tolerate sharp temperature fluctuations or excessive rainfall during the growing season. Late summer dryness is necessary for proper maturation of the spikes, which must be picked within a few days of full ripeness, otherwise they are prone to shattering, and the lupulin quality is inferior. After harvesting, hops are dried in warm air kilns for several hours, cooled or cured in another building for about a week to equalize moisture content in the various pickings, baled, and marketed.

In former times hops have been used medicinally as multipurpose tonics and to treat certain types of epidermal sores and irritations, usages perhaps related to the bacteriostatic quality of the resin. In Scandinavia phloem fibers from the aërial stems of *H. Lupulus* are made into twine and cloth to a limited extent. *Humulus japonicus* is occasionally used as an ornamental plant.

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of the fruiting spike, and *Cannabis sativa* × *H. Lupulus* and *H. Lupulus* × *H. japonicus* crosses (fruits matured but contained aborted embryos).]

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NOTES RELATING TO THE FLORAS OF NORFOLK AND LORD HOWE ISLANDS, I.

P. S. GREEN

IN OCTOBER AND NOVEMBER 1963 I had the good fortune to visit first Norfolk Island and then Lord Howe Island in the southwestern Pacific, and to spend about a week on each, making botanical collections and observations upon the flora. The visits were made possible through funds from the Arnold Arboretum (where, at the time, I had the honor of being a staff member) and from the National Science Foundation (Grant No. GB1545), and grateful acknowledgement is made for their generous support. The immediate reason for the visits to these islands was to see certain members of the family *Oleaceae*, but the opportunity was taken to examine the general flora.

Like most oceanic islands, Norfolk and Lord Howe are noted for the high degree of endemism in both their flora and fauna. In fact, they have been referred to as "two of the most interesting oceanic islands in the world" (Good, 1964, p. 144) and as such are of particular interest to biogeographers. But biogeography must be based on accurate taxonomy and when naming the collections made on the islands it soon became clear that the existing floristic lists are quite out of date (Laing, 1915; Oliver, 1917) and that a considerable amount of work upon these floras still remains to be done, especially when the plants are considered in relation to those of the various adjacent land-masses and islands. Because of this I am gradually working over the whole vascular flora of the two islands, examining it carefully, comparing specimens with related material from Australia, New Zealand, New Caledonia, and elsewhere, and reassessing their taxonomy. Due to many other commitments this work has not progressed as rapidly as I had hoped but I have been urged to publish at least the conclusions so far reached.

LEGUMINOSAE

Sophora howinsula (W. R. B. Oliver) P. S. Green, comb. nov.

Edwardsia chrysophylla sensu C. Moore, Sketch of the Vegetation of Lord Howe Island 3.1869 & in E. S. Hill, Lord Howe Island: Official Visit by the Water Police Magistrate and the Director of the Botanic Garden, Sydney 28. 1870, *non* Salisb.

Sophora tetraptera sensu F. Muell. Fragm. Phytogr. Austral. **7**: 26. 1869 & **9**: 77. 1875; sensu C. Moore & Betche, Handb. Fl. New S. Wales 519. 1893; sensu Tate in Fletcher, Macleay Mem. Vol., Linn. Soc. New S. Wales 217. 1893; sensu Hemsley, Ann. Bot. **10**: 235. 1896; sensu Maiden, Proc. Linn. Soc. New S. Wales **23**: 128. 1898; *non* J. Miller.

S. tetraptera J. Mill. var. *howinsula* W. R. B. Oliver, Trans. & Proc. New Zealand Inst. **49:** 139. 1917. Type: Lord Howe Island, Transit Hill, 1917, *W. R. B. Oliver* (? WELT, not seen).

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Yakovlev has recently published a synopsis of the genus *Sophora* (Yakovlev, 1967) in which he includes the Lord Howe representative as a subspecies of the New Zealand *S. tetraptera*, in sect. EDWARDSIA (Salisb.) Taub.[1] He recognizes ten species in this section, together exhibiting a most interesting distribution: *S. denudata* Bory from Réunion; *S. chrysophylla* (Salisb.) Seem. from Hawaii; *S. macrocarpa* Sm. from Chile; *S. fernandeziana* (Phil.) Skottsb., *S. masafuerana* (Phil.) Skottsb., and *S. reediana* (Phil.) Yakovlev from the Juan Fernandez Islands; *S. toromiro* (Phil.) Skottsb. from Easter Island; and *S. microphylla* Ait. and *S. tetraptera* J. Mill. from New Zealand, except for subsp. *macnabiana* (R. Graham) Yakolev, a Chilean plant which he includes under *S. microphylla*, and the Lord Howe Island plant which he places as a subspecies of *S. tetraptera*.

Careful examination of the Lord Howe material at Kew leads me to believe that specific recognition for this plant is justified. Certainly the number and type of differences from the New Zealand *S. tetraptera* are of a comparable order with those from *S. microphylla* and *S. chrysophylla*. On the other hand the other subspecies which Yakovlev recognizes in this section, subsp. *macnabiana*, seems closer to the New Zealand material of *S. microphylla*, under which he places it, than do the Lord Howe Island specimens to *S. tetraptera*.

The differences noted are as follows. Leaves with fewer leaflets (9–)13–17(–19) as opposed to (17–)19–33(–39) in *S. tetraptera*, slightly larger (1.3–)1.7–2.5(–3.5) by (0.6–)0.8–1(–1.3) cm. in contrast to (0.6–)1–2(–3) by (0.3–)0.5–0.7(–1) cm., and glabrous above even in the slightly sunken midrib. Flowers smaller 2.8–3.5 cm. long (4–5 cm. long in *S. tetraptera*); calyx smaller 0.7–0.8 cm. long, not 1–1.5 cm., lightly, not densely hairy; standard a little shorter (2 cm. long) than the keel (2.5 cm. long) in contrast to 3–3.5 cm. and 4–5 cm. in *S. tetraptera*. Fruit with the surface of each segment minutely warty or uneven in contrast to smooth in the New Zealand plant.

Lord Howe Island. Without locality, ex Phytologic Museum of Victoria (K), *Milne* (K), *C. Moore 10* (K) & Oct. 1936, *McComish 19* (K); Transit Hill, low dryish forest, 12 Nov. 1963, *Green 1616* (A, K); Transit Hill, in dense shrubbery, common, approx. 125 m. alt., 17 July 1965, *van Balgooy 1014* (K).

[1] Yakovlev, like other authors, attributes this section to Seeman (Fl. Vit. 66. 1865). However, although Seeman sunk the genus *Edwardsia* Salisb. under *Sophora* L. he did not propose it formally as a section. The earliest authority to do this that I have traced is Taubert in Engler & Prantl, Nat. Pflanzenfam. III. 3: 195. 1888. E. G. Baker (in Hook. fil. Fl. Brit. Ind. 2: 251. 1878, where in most cases he carefully designates "Subgen." and "Sect.") uses an unspecified infrageneric category denoted by "§".

MALVACEAE

Sida zahlbruckneri Rech.

In 1907 Rechinger published the name *Sida zahlbruckneri*, attributing the species to Lord Howe Island and basing it upon a MacGillivray collection at Vienna. There has been no other record of this species and, through the kindness of the Director of the Naturhistorisches Museum, to whom grateful thanks are expressed, I have been enabled to examine the holotype on loan. It is clear that it has unfortunately been mislabelled at some time and that it was collected on the Isle of Pines, New Caledonia, and not Lord Howe Island. The particular MacGillivray collections of which it forms a part, were made, along with others by W. G. Milne, on the voyage of H.M.S. *Herald*, 1853–4. They were sent by MacGillivray and Milne to Kew and examination of the herbarium there reveals nothing resembling this species from Lord Howe Island, but both collectors made specimens of an identical *Sida* from the Isle of Pines, the next island visited by the *Herald* after leaving Lord Howe (Observatory Island, Isle of Pines, banks by the shore, Sept. 1853, *MacGillivray 824*, & Observatory Island, Isle of Pines, on beach, abundant, Oct. 1853, *Milne 85*). On comparing the specimens it is clear that the type of *S. zahlbruckneri* agrees exactly with these collections and must have been part of them before becoming separated and mislabelled.

In 1892 E. G. Baker in his "Synopsis of *Malveae*" described *Sida nummularia*, based on the Milne collection cited above, and, therefore, not only is *S. zahlbruckneri* no longer to be classed as one of the Lord Howe Island endemics, but in fact falls into synonymy.

Sida nummularia Bak. f. Jour. Bot. **30**: 290. 1892; Däniker, Viert. Naturf. Ges. Zürich **78** (Beibl. 19): 261. 1933; Guillaumin, Fl. Nouv.-Caléd. 209. 1948. Type: Isle of Pines, New Caledonia, *Milne 85* (K).

S. zahlbruckneri Rech. Repert. Sp. Nov. **4**: 228. 1907. Type: "Lord Howe Island" [Isle of Pines, New Caledonia], *MacGillivray* (W).

Sida nummularia, which is endemic to New Caledonia, is very similar to *S. parvifolia* DC. (Prodr. 1: 461. 1824) based on a specimen from Réunion and widespread on the Mascarene Islands. In fact they may not be specifically distinct; however, although the 34 collections I have examined from Mauritius, the Seychelles, and the Cosmoledo and Chagos Archipelagoes (I have not actually seen a specimen from Réunion) show considerable variation, the 11 New Caledonian collections seen are very consistent in leaf shape and size. Moreover, in each case where ripe fruit was examined, the seed of the Pacific plant was found to be puberulent at the apex, near the slit in the mericarp wall, but glabrous in the plants from the western Indian Ocean. The exact status of these two species (as well as *S. discolor* Bak. f., *non* Hook., described from "Timor" [Sumba]) must await careful biosystematic work on the group.

Van Borssum Waalkes (in Blumea **14**: 192, 193. 1966) equates *Sida dis-*

color Bak. f. with *S. parvifolia* DC. and says that "it has been found on the Pacific Islands." No material is cited but it seems possible that these New Caledonian collections, together with others from Fiji, Tonga, and Samoa are involved. The specimens from these three latter groups of islands belong to *S. samoensis* Rech. (*S. microphylla* sensu Benth. in Hook. London Jour. Bot. 2: 211. 1843, & sensu Seem., Fl. Vitiensis 15. 1865, *non* Cav.) which is superficially very similar and also recorded from coral beaches, but with mericarps which are clearly biaristate, as pointed out by Däniker (Viert. Naturf. Ges. Zürich **78** (Beibl. 19): 261. 1933).

OXALIDACEAE

Oxalis corniculata L. Sp. Pl. 435. 1753; Oliver, Trans. & Proc. New Zealand Inst. **49**: 140. 1917.

Var. **corniculata.**

O. reptans Sol. ex Forst. f. Prodr. 90. 1786, *nom. nud.*; Endlicher, Prodr. Fl. Norf. 72. 1833, *nom. nud.*

O. corniculata L. var. *reptans* Laing, Trans. & Proc. New Zealand Inst. **47**: 28. 1915. Type: Norfolk Island, on rocks, particularly near sea shore, 1912, *Laing* (CANTY).

Norfolk Island. Anson Bay, 6 Jan. 1939, *McComish 122* (K).

Lord Howe Island. Near cultivated ground, Sept. 1853, *MacGillivray 719* (K). Southeastern slopes of Malabar, dry open rocky and grassy patches in low forest, 11 Nov. 1963, *Green 1559* (A, K); behind beach, Ned's Beach, 5 m. alt., 20 July 1965, *van Balgooy 1054* (K).

Var. **microphylla** Hook. f. Fl. Nov.-Zeland. 1: 42. 1852 & Fl. Tasm. 1: 59. 1855; Young, Watsonia **4**: 56. 1958; Allan, Fl. N. Zeal. 1: 239. 1961; Hoogland in Turner *et al.* Austral. Conservation Foundation Spec. Publ. 1 (The Conservation of Norfolk Island): 34. 1968. Types: New Zealand, Whaapu, Bay of Islands, 1833, *R. Cunningham 234* (*A. Cunningham 587*) (K); Tasmania, *A. Cunningham 1837/94* & Glen Leith, 14 Sept. 1840, *J. D. Hooker* (K).

Norfolk Island. Near Kingston, alongside creek, 28 Jan. 1939, *McComish 122A* (K). Kingston, ruins of old prison, 30 Oct. 1963, *Green 1434* (A). Near Rocky Point, earthy banks and ledges on sea cliffs, 30 Oct. 1963, *Green 1461* (A). Phillip Is., eroded and rabbit infested hillside, 31 Oct. 1963, *Green 1502* (A).

The world-wide weed var. *corniculata* has been introduced to both Lord Howe and Norfolk Islands, but var. *microphylla* is most probably native on the latter. Captain Cook, when describing the discovery of the island in 1774, wrote that he found "cabbage-palm, wood-sorrel, sow thistle and samphire abounding in some places on the shores" ("A voyage towards the South Pole and round the world" 2: 148. 1777 & in "The three voyages of Captain James Cook round the world" **4**: 137. 1821). It is probably this species that he refers to as wood-sorrel (although it is not

the *Oxalis* he might have known in Britain). In reference to the island, he also stated (*op. cit.* 147 & 136) that "we found it uninhabited, and were undoubtedly the first that ever set foot on it." Yet, whether his party were, in fact, the first to land on the island may be open to question, even if it was uninhabited when they discovered it. Sow thistle, *Sonchus oleraceus*, now a widespread weed, is generally considered native in the European, W. Asian and Mediterranean regions and must, therefore, have been introduced to Norfolk Island before Capt. Cook's visit. Governor King, then Lieutenant (in Hunter, "A Historical Journal of the Transactions at Port Jackson and Norfolk Island" 306. 1793), stated that on 5th April, 1788, in "a fine valley . . . . a number of plantain or banana tree" were found and later (p. 396) that "those planted out . . . . have already yielded good fruit." Although Endlicher (*l. c.* : 35) thought that *Musa* was indigenous he was probably mistaken. The island was previously probably inhabited, with the bananas planted and the sow thistle introduced (and the wood-sorrel?). (See also Thorpe in Jour. Polynesian Soc. **150**: 123–126. 1929 and McCarthy, *op. cit.* 172: 267–270. 1934, for further evidence of previous occupation of the island.)

Although var. *microphylla* is stated by Young (1958, p. 56) to be native of the "mountainous parts of New Zealand and Tasmania" the very sparse field notes on the material in the herbarium at Kew give little or no indication that this may be its habitat. Allan (1961, p. 239) says that the distribution is uncertain and that the variety occurs in North Auckland and I have certainly seen both varieties almost at sea-level on Norfolk Island.

Although Laing (1915, p. 28) gives the first valid description to go with Solander's epithet *reptans* it is clear that he bases it on the plant from Norfolk Island which, in a footnote, he says may be endemic. Before examining his type material, kindly sent on loan, I had expected it to be the small leaved var. *microphylla*; but I have been surprised to find that it proves to be var. *corniculata* although a semiprostrate, small-leaved form. Similarly, the specimen at the British Museum of the plant collected in New Zealand by Banks and Solander is a prostrate form of var. *corniculata*. Var. *microphylla* is recorded from both New Zealand and Tasmania and, from the material I have seen, is somewhat variable in pubescence. However, it seems to maintain its decumbent habit, very small leaves (less than 5 mm. long), short capsule (less that 12 mm. long), and small seeds (1 mm. or less in length). I have examined material of *Oxalis corniculata* from most parts of the world but have found var. *microphylla* from Norfolk Island, New Zealand, and Tasmania only, except for some specimens from Britain, where it is recorded as "a frequent garden escape" (Young 1958).

RUTACEAE

Acronychia J. R. & G. Forst.

A critical examination of the Norfolk and Lord Howe Island plants

that have passed under the names *Acronychia baueri* and *A. endlicheri*, together with the related plants from the mainland of Australia and islands in the Pacific, has led to a reassessment of the whole group. It is concluded that two species are involved, one consisting of three geographical subspecies and the other endemic to New Caledonia. They may be identified by the key below.

It is possible that the plant described as *Acronychia acidula* F. Muell. (Fragm. Phytogr. Austral. **4**: 154. 1864) is another subspecies, but no flowering material has been seen. It occurs in tropical parts of Queensland (type locality: Seaview Range, Rockingham Bay) and has much larger leaves and fruit. Similarly, *A. vestita* F. Muell. (*l. c.* 155. 1864), of which I have seen only fruiting material may be another subspecies. It was also described from the Rockingham Bay area and the two taxa were combined by F. M. Bailey (Queensland Fl. 1: 210. 1899), but the isotypes and other material I have examined at Kew differ so much in indumentum that they may prove to be distinct.

KEY TO ACRONYCHIA SIMPLICIFOLIA AND A. LEIOCARPA

1. Leaves usually more than 8 cm. long, (4.5–)7–13(–16) cm. long; petioles (1–)2–4(–5) cm. long; calyx 1.5–2.5 cm. long; ovary and fruit hairy or velutinous; fruit apex at least slightly pointed. ..... *A. simplicifolia.*
   2. Apex of leaf rounded or obtuse, retuse or subretuse; fruit apex slightly beaked or distinctly pointed.
      3. Petiole glabrous or minutely pubescent when young, eventually glabrate; leaves ovate-elliptic; fruit only slightly hairy and slightly beaked. ..... subsp. *simplicifolia.*
      3. Petiole pubescent, sometimes glabrous with age; leaves elliptic; fruit subvelutinous, distinctly pointed. ..... subsp. *neo-scotica.*
   2. Apex of leaf acute, sometimes rounded subacute; fruit apex slightly pointed, more or less pinched; petiole minutely puberulent when young. ..... subsp. *petiolaris.*
1. Leaves less than 8 cm. long, (2–)3–7(–8) cm. long; petioles (0.8–)1–1.7(–2) cm. long; calyx 1–1.5 mm. long; ovary and fruit glabrous; fruit apex not beaked or pointed. ..... *A. leiocarpa.*

Acronychia simplicifolia (Endl.) McGillivray & Green, comb. nov.

Vepris simplicifolia Endl. Prodr. Fl. Norf. 89. 1833. Type: Norfolk Island, Dec. 1804, *Bauer* (W, not seen).

Acronychia simplicifolia (Endl.) Steud. Nom. ed. 2. **1**: 21. 1840, *nomen in synon.*; Hoogland in Turner *et al.* Austral. Conservation Foundation Spec. Publ. **1** (The Conservation of Norfolk Is.): 34. 1968, *nomen.*

Subsp. **simplicifolia.** FIGURE 1a.

Acronychia endlicheri Schott, Rutaceae. Fragm. Bot. 3. *t.* 2. 1834, *nom. illegit.*; F. Muell. Fragm. Phytogr. Austral. **9**: 103. 1875; Moore & Betche, Handb. Fl. New S. Wales 518. 1893; Tate in Fletcher, Macleay Mem. Vol., Linn.

Soc. New S. Wales, 217. 1893; Maiden, Proc. Linn. Soc. New S. Wales **28:** 699. 1903; Laing, Trans. & Proc. New Zealand Inst. **47:** 29. 1915. Type as for *Vepris simplicifolia* Endl.

A. baueri Schott, *op. cit.* 5. *t.* 3. 1834; Benth. Fl. Austral. **1:** 366. 1863; F. Muell. Fragm. Phytogr. Austral. **9:** 77 & 103. 1875; F. M. Bailey, Syn. Queensl. Fl. 54. 1883; Moore & Betche, Handb. Fl. New S. Wales 49. 1893; Tate in Fletcher, Macleay Mem. Vol., Linn. Soc. New S. Wales 217. 1893; Hemsl. Ann. Bot. **10:** 233. 1896; Maiden, Proc. Linn. Soc. New S. Wales **23:** 124. 1898; F. M. Bailey, Queensl. Fl. 208. 1899 & Compreh. Cat. Queensl. Pl. 81. 1913; Oliver, Trans. & Proc. New Zealand Inst. **49:** 141. 1917; Francis, Austral. Rain Forest Trees 167. 1929 & ed. 2. 191. 1951; Anderson, Trees New S. Wales ed. 2. 231. 1947 & ed. 4. 210. 1968; Beadle *et al.* Handb. Vasc. Pl. Sydney Distr. 322. 1963. Type: Locality unknown, ? Norfolk Island, *Bauer* (? W, not seen).

A. ovata Endl. ex. Heynh. Nom. **2:** 8. 1846, *nom. nud.*

A. hillii F. Muell. Fragm. Phytogr. Austral. **1:** 26. 1858. Type: Queensland, Moreton Bay, *Hill & F. Mueller* (MEL, not seen).

Jambolifera endlicheri (Schott) Kuntze, Rev. Gen. Pl. 102. 1891.

J. baueri (Schott) Kuntze, *loc. cit.* 1891.

Bauerella australiana Borzi, Bol. Orto Bot. Palermo **1:** 155. 1898, *nom. illegit.* Type: as for *Acronychia baueri* Schott.

Acronychia baueri Schott f. *majoriflora* Domin, Bibl. Bot. **22** (89) (Beitr. Fl. Pflanzengeogr. Austral.: 848): 294. 1927. Type: Queensland, Brisbane River, *Dietrich* (not seen).

Bauerella baueri (Schott) Däniker, Viert. Naturf. Ges. Zürich **77** (Beibl. 19): 202. 1932, *quoad typ.*

Norfolk Island. Apr. 1835, *Backhouse 616* (K); margins of woods, June 1830, *A. Cunningham 29* & *148* (K); above Red Stone, 25 Aug. 1968 & 8 Mar. 1969, *Owen Evans* (K).

Lord Howe Island. *Fullager* (K); 1869, *C. Moore 17, 32* & *48*(K); low dry forest, southeast lower slope of Malabar, 11 Nov. 1963, *Green 1574* (A, K).

Queensland. North Kennedy district: Strathdickie, *Michael 1356* (GH); Rockingham Bay, *Dallachy* (K). South Kennedy district: Forest reserve 652 Cauley, approx. 30 miles S. of Proserpine, 22 May 1967, *Mackay 67/144* (K); Dalrymple Heights, rain forest, Aug.–Oct. 1947, *Clemens* (GH, K). Port Curtis district: Middle Percy Island, Jan. 1906, *Tryon* (A); Northumberland Islands, *R. Brown "5328"* (K). Wide Bay district: Mt. Perry, Aug. 1912, *Boorman* in *NSW 16272* (K); Nikenbah, *Tryon* (A); Kin Kin, Jan. 1916, *White* (K). Moreton district: Blackall Range, Dec. 1916, *White* (A); Forest reserve, Yarraman, 1400 ft. alt., Aug. 1944, *Clemens* (A); Mt. Glorious, ridge forest, 2000 ft. alt., Jan. 1945, *Clemens* (GH, K), & common in rain forest, 28 June 1937, *White 11078* (K); Mt. Mistake, 3000 ft. alt., 2 Feb. 1944, *Clemens 43591* (A); Brisbane R., *A. Cunningham* (GH), 1829, *Fraser 157, 183* & *213* (K) July & Aug. 1855, *F. Mueller* (K) & dark, dry woods, July, *A. Cunningham 3* (K); Tambourine Mt., Oct. 1909, *Simmonds* (A); Moreton Bay, Oct. 1824, *A. Cunningham 18* (K).

New South Wales. Upper Eungella, Tweed River, June 1923, *White 13268* (A); Tweed Heads, Sept. 1910, *Simmonds* (A); Richmond R., *C. Moore* (K); Lismore, Aug. 1891, *Maiden* (A); Carrai Carrai State Forest, 30 miles approx. W. of Kempsey, frequent on limestone ridge, 810 m. alt., 11 June 1958, *Con-*

stable in *NSW 46231* (K); Port Macquarie. May 1819, *A. Cunningham 49* (K); W. of Coneac (Manning R., approx. 18 miles NW. of Gloucester), small rain forest pocket by creek, 15 Oct. 1953, *Johnson* in *NSW 26274* (K); 16 miles ENE. of Singleton, patch of broad-leafed forest, 27 Mar. 1960, *Storey 7203* (K); Ash Islands, Newcastle, 1802–5, *R. Brown "5329"* (K); Wyong, Dec. 1898, *Boorman* (A); Illawarra, Nov. 1818, *A. Cunningham 169* & Aug. 1824, *A. Cunningham 4* (K); 1 mile W. of Central Tilba, very common in a dry type of rainforest on rocky hillside, 9 Sept. 1960, *Johnson & Constable* in *NSW 52308* (K); slopes of Mt. Dromedary, Central Tilba (approx. SW. of Narooma), occasional in rain forest, 90 m. alt., 12 Sept. 1953, *Constable* in *NSW 26537* (K); Milton, on igneous rock, 5 Dec. 1905, *Cambage 1420* in *NSW 26312* (A, K).

A careful examination of the Norfolk and Lord Howe Island plants shows that they do not differ taxonomically from that of the eastern mainland of Australia, from Queensland and New South Wales.

When taken in the context of the Tribe *Toddalieae* the characters used by Borzi to define the genus *Bauerella* are insufficiently distinct to justify generic separation. Unfortunately Borzi failed to take up the epithet *baueri*, although citing it in synonymy, and thus rendered his binomial illegitimate. The correct combination *B. baueri* is sometimes attributed to Engler (in Engler & Prantl, Nat. Pflanzenfam. Nachtr. II–III. **4**: 35. 1900) but it is not actually made by him at this reference. The earliest valid use that has been traced is that of Däniker referred to above.

My friend and colleague D. J. McGillivray quite independently, and in connection with his work on the plants of New South Wales, came to the realization that the combination *Acronychia simplicifolia* had never been validly made and so I have pleasure in sharing with him in the combination above.

Subsp. **neo-scotica** P. S. Green, subsp. nov., a subsp. *simplicifolia* petiolis pubescentibus, foliis constanter ellipticis et fructibus subvelutinis manifeste acutis differt. FIGURE 1b.

Acronychia eriocarpa Panch. ex. Guillaum. Not. Syst. Paris **2**: 98. 1911, *nom. in synon.* & in Ann. Mus. Col. Marseille **II. 9** (Cat. Pl. Phan. Nouv.-Caléd. **1**: 39): 111. 1911, *nom. nud.*

A. baueri sensu Guillaum. *ll. cc.* (1911), *non* Schott.

Bauerella australiana sensu Guillaum. *ll. cc.* 40 & 112. 1911 & Jour. Arnold Arb. **12**: 235. 1931, *non* Borzi.

B. baueri sensu Däniker in Viert. Naturf. Ges. Zürich **77**(Beibl. 19): 202. 1932, *pro parte, excl. spec. typ.*; sensu Guillaum. Fl. Nouv.-Caléd. 168. 1948.

New Caledonia. Montaignes de Wailiou, 1861–67, *Vieillard 2704* (K); Nouméa, 1868–70, *Balansa 376* (K); Nouméa (Ouen Toro), 3 Aug. 1930, *Franc 2454* (A, K); dry stony slopes on Ouen Toro, 0–50 m. alt., 26 Feb. 1955, *McKee 2163* (K); Anse Vata, low calcareous hill, 10 July 1955, *McKee 2731* (A); Mt. Dore, 1855–60, *Vieillard 859* (K); "auf den Hügeln bei Yaouhé," 17 Oct. 1902, *Schlechter 15071* (K); Prony, *Franc* (K); Port-Boisé, 1861–67, *Deplanche 511* (K, holotype) & *Deplanche 510* (A).

New Hebrides. Eromanga, Cook's Bay, 22 July 1896, *A. Morrison* (K). Anei-

tyum: Anelgauhat, 5 June 1896, *A. Morrison* (K); Anelgauhat Bay, rain forest, common, 305 m. alt., 14 Feb. 1929, *Kajewski 761* (A, K).

This subspecies is most easily distinguished from the type by its fruit, which is fine velvety and relatively long pointed and rounded in section below the apex. In subsp. *simplicifolium*, as well as the fruit being only scattered hairy or glabrate, it is much less prominently pointed and in transverse section below the apex shows four distinct indentations (FIGURES 1a & b). Also the petiole in this subspecies is more pubescent than in the others.

The epithet chosen alludes to the fact that it occurs in both New Caledonia and the New Hebrides.

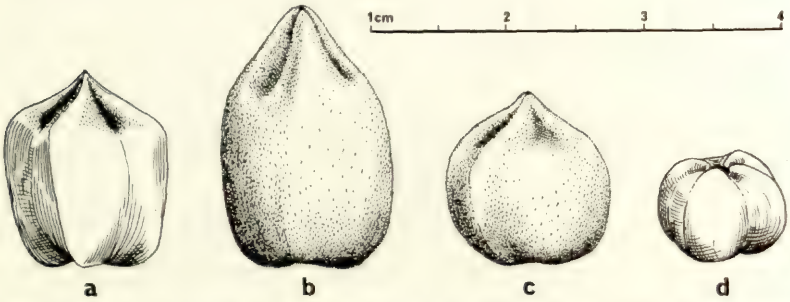

FIGURE 1. *Acronychia* fruits, all × 2. a, *A. simplicifolia* subsp. *simplicifolia* (from *Johnson & Constable NSW 52308*); b, subsp. *neo-scotica* (from *Kajewski 761*); c, subsp. *petiolaris* (from *Horne 1114*); d, *A. leiocarpa* (from *McKee 2115*).

Subsp. **petiolaris** (A. Gray) P. S. Green, comb. nov. FIGURE 1c.

Acronychia petiolaris A. Gray, Bot. U.S. Expl. Exped. **1:** 335. 1854 & *t. 33A*. 1857; Seem. Fl. Vitiensis 31. 1865; Gibbs, Jour. Linn. Soc. Bot. **39:** 142. 1909; Smith, Jour. Arnold Arb. **32:** 243. 1951; Parham, Pl. Fiji Is. 164. 1964. Type: Fiji, Mathuata, *U.S. Exploring Expedition* (GH, holotype).

Jambolifera petiolaris (A. Gray) Kuntze, Rev. Gen. Pl. 102. 1891.

Fiji. VANUA LEVU. Mbua: southern portion of Seatovo Range, 100–350 m. alt., dry forest, 20 Apr.–2 May 1934, *Smith 1702* (A, K); Bua, forest, not common, Sept. 1878, *Horne 1114* (GH, K). Mathuata: without locality, *U.S. Exploring Expedition* (GH, holotype of subsp. *petiolaris*); Dreketi, forest, *Parham, Qoro & Kuruvoli* in *Dept. Agric. 13451* (K); Dreketi district, near village Basakalave, 32 km. W. of Seaqaqa, 40 m. alt., lateritic hill, rather dense forest, 26 Mar. 1964, *Staufer & Kuruvoli 5844* (K); Wainunu-Ndreketi divide, 200–300 m. alt., dense forest, 17 May 1934, *Smith 1841* (A, K); Seaqaqa, coffee plantation, 27 Feb. 1964, *Parham & Kuruvoli* in *Dept. Agric. 13908* (K); Seanggangga Plateau, in drainage of Korovuli R., vicinity of Natua, 100–200 m. alt., patches of forest in open rolling country, 25 Nov.–8 Dec. 1947, *Smith 6711* & *6728* (A, K); southern base of Mathuata Range, N. of Natua, 100–250 m. alt., dense forest, 1–4 Dec. 1947, *Smith 6779* (A, K); southern slopes of Mt. Numbuiloa, E. of Lambasa, 100–350 m. alt., open forest, 27 Oct.–10 Nov. 1947, *Smith*

6407 (A, K); Lambasa, approx. 200 ft. alt., 17 Dec. 1922, *Greenwood 566* (K); Nasuaca, forest, *22* July 1963, *Qoro & Kuruvoli* in *Dept. Agric. 13486* (K). VITI LEVU. Mba: Nandarivatu, 2600 ft. alt., 11 Mar. 1927, *Mead* in *SFN 1987* (K) & 3000 ft. alt., in copse, June 1927, *Tothill 54* (K); vicinity of Nandarivatu, 850 m. alt., *22* Nov. 1927, *Gillespie 3984* (GH), & 900 m. alt., 14 Dec. 1927, *Gillespie 4311* (K); Sovutawambu, 5 miles from Nandarivatu, 750–800 m. alt., *27* Feb.–4 Mar. 1941, *Degener 14652* (A, K); southern slopes of Mt. Ndelainathovu, on the escarpment W. of Nandarivatu, 870–970 m. alt., dense forest, *26* June 1947, *Smith 4934* (A, K); hills between Nandala & Nukunuku Creeks, along trail from Nandarivatu toward Lewa, 750–850 m. alt., thickets on fairly open slopes, *22* Sept. 1947, *Smith 6150* (A, K). KANDAVU: understory in rainforest, *Watkins 750* (K). Without locality: *Horne 599* (GH, K).

The Fijian plant resembles subsp. *neo-scotica* in its fruit, which is not quite so pointed and is less completely rounded in section below the apex. But the leaf shape, however, is consistently different with an acute apex, rarely only subacute, never retuse or subretuse, and usually with more primary veins on each side of the midrib: (7–)9–10(–12) per side in contrast to (6–)7–9(–11) in the other subspecies.

Acronychia leiocarpa P. S. Green, sp. nov., a *A. simplicifolia* foliis minoribus, (2–)3–7(–8) cm. longis, ovariis glabris, et praesertim fructibus minoribus glabris differt. FIGURE 1d.

A. baueri sensu Pancher in Sebert & Pancher, Not. Bois Nouv. Caléd. 245. [1874], *non* Schott.
A. ligustroides Panch. ex Guillaum. Not. Syst. Paris **2**: 98. 1911. *nom. in synon.* & Ann. Mus. Col. Marseilles **II.9** (Cat. Pl. Phan. Nouv.Caléd. **1**: 40): 112. 1911, *nom. nud.*
A. ovalifolia Panch. ex Guillaum. *ll. cc.* 1911, *nom. nud.*

Small *tree* to 5 m. tall, branchlets puberulent when young becoming glabrous. *Leaves* simple; *petioles (0.8–)1–1.7(–2) cm. long*, minutely puberulous; lamina elliptic or slightly elliptic-ovate, *(2–)3–7(–8) cm. long*, by (1.5–)2–3(–3.5) cm. broad, glabrous; margin entire; apex rounded, retuse; base obtuse and more or less rounded or acute; *venation finely and clearly raised reticulate* above and below, 7–9(–10) primary nerves on each side of the midrib. *Inflorescence* axillary, condensed paniculoid, (0.5–)1–2(–2.5) cm. long, (1–)3–15-flowered, puberulent; flowers hermaphrodite, green or yellowish green; pedicels 0–1 mm. long. *Calyx* minutely tomentose externally, *lobes 4, 1–1.5 mm. long*, triangular ovate. *Corolla* valvate, minutely tomentose externally, lobes 4, 2.5–3.5 mm. long. *Stamens* 8, antesepalous 1.5–2 mm. long, antepetalous 1–1.5 mm. long; filaments flat, ciliate 0.7 mm. broad, abruptly tapered at the apex; anthers 0.5 mm. long. *Ovary glabrous*, 4-loculate, with several axile ovules; style arising from a slight depression on the top, 0.8 mm. long with somewhat flattened terminal stigmatic area 0.7 mm. in diameter. *Fruit glabrous*, rounded but more or less cuboid, apex not pointed, with 4 indentations (FIGURE 1d), red (fide *McKee 2115*), 0.6–1 cm. long and

broad, endocarp hard boney, ? indehiscent, with 2–3 black seeds per loculus.

New Caledonia. Wailou, 1861–67, *Vieillard 200* (K); Nouméa, 1868–70, *Balansa 375* & *375a* (K); Bois de Port-Despointes (Nouméa), "bois secs des collines littorales, schistes nummulitiques," 14 Nov. 1942, *Virot 810* (A), *812* (A) & *822*(A); foot of Ouen Toro, 10 m. alt., 13 Feb. 1955, *McKee 2115* (A, K); NE. slope of Ouen Toro, Nouméa, dry scrub, 26 Sept. 1963, *Green 1211* (A, isotype; K, holotype); Isle des Pins, "ad rivulum ad pedem Pic Nga." 100 m. alt., 18 July 1965, *Bernardi 10067* (K); without locality, 1862, *Pancher s.n.* & *Deplanche 491* & *510* (K); "pieds de Ma . . . ," 1900–1910, *Le Rat 2273* (A).

Acronychia leiocarpa has been confused with *A. simplicifolia*. Both species occur together, e.g. *McKee 2115* and *2163* were both collected on Ouen Toro near Nouméa, and it would be interesting to investigate their biology. However, *A. leiocarpa* is immediately separable by characters of the leaf, its smaller size and finer reticulation, and, above all, by the glabrous ovary and subsequent fruit. Other characters for separation are found in the smaller size of the flower parts, the relatively broad staminal filaments, which are usually more abruptly contracted below the anther, and the smaller, unpointed fruit (FIGURE 1D).

It appears that at one time Pancher recognized that this species was distinct and proposed the names *Acronychia ligustroides* and *A. ovalifolia* which he attached to some of his herbarium specimens, but in Sebert & Pancher "Notice sur les Bois de la Nouvelle Calédonie" 245 [1874], although describing the characteristic fruit, he equated this species with the Australian *A. simplicifolia* (as *A. baueri*). Guillaumin (in Not. Syst. Paris **2**: 98. 1911) discussed Pancher's proposed species and mentioned the glabrous ovary and abruptly narrowed staminal filaments (by inference from his description of the filament of *A. simplicifolia*) but he nevertheless seems to have concluded that only one species was involved.

Zanthoxylum L.

The plants that have passed under the names *Blackburnia pinnata*, *Zanthoxylum blackburnia*, *Fagara pinnata*, etc., also need reassessment, with the recognition of a new species from New Caledonia.

Zanthoxylum pinnatum (J. R. & G. Forst.) W. R. B. Oliver, Trans. & Proc. New Zealand Inst. **49**: 140. 6 July 1917; Druce, Rep. Bot. Exch. Club Brit. Is. **4**: 653 [? Sept.] 1917; A. C. Smith, Bull. Bishop Mus. **141**: 76. 1936; Hoogland in Turner *et al.* Austral. Conservation Foundation Spec. Publ. 1 (The Conservation of Norfolk Island): 34. 1968. Type: Norfolk Island, *J. R. & G. Forster* (BM, K).

Blackburnia pinnata J. R. & G. Forst. Gen. Char. 12. *t. 6.* 1776; Forst. f. Prodr. 10. 1786; DC. Prodr. **2**: 83. 1825; Endl. Prodr. Fl. Norfolk. 88. 1833; A. Cunn. in Heward, Hook. Lond. Jour. Bot. **1**: 113. 1842.
Ptelea pinnata (J. R. & G. Forst.) Linn. f. Suppl. Pl. 126. 1781.

Samara blackburnia Spreng. Syst. Veg. **1:** 441. 1824, *nom. illegit.*

Zanthoxylum blackburnia Benth. Fl. Austr. **1:** 363. 1863; Hemsl. Ann. Bot. **10:** 233. 1896; Burkill, Jour. Linn. Soc. Bot. **35:** 30. 1901; Laing, Trans. & Proc. New Zealand Inst. **47:** 29. 1915; *nom. illegit.*

Xanthoxylon blackburnia C. Moore, Sketch of the vegetation of Lord Howe Island 3.1869 & in E. S. Hill, Lord Howe Island: Official Visit by the Water Police Magistrate & the Director of the Botanic Gardens, Sydney 8. 1870; C. Moore & Betche, Handb. Fl. New S. Wales 518. 1893; Tate in Fletcher, Macleay Mem. Vol., Linn. Soc. New S. Wales 215. 1893; Maiden, Proc. Linn. Soc. New S. Wales **28:** 699. 1903; *nomen.*

Xanthoxylon howeanum F. Muell. Fragm. Phytogr. Austral. **9:** 77. 1875, *nom. nud.*; Tate in Fletcher, Macleay Mem. Vol., Linn. Soc. New S. Wales 215. 1893, *nom. nud.*

Fagara pinnata (J. R. & G. Forst.) Engl. in Engl. & Prantl, Pflanzenfam. III. **4:** 119. 1896, & ed. 2 **19a:** 224. 1931; A. C. Smith, Jour. Arnold Arb. **32:** 227. 1951; Yuncker, Bull. Bishop Mus. **220:** 151. 1959.

F. gillespieana A. C. Sm. Jour. Arnold Arb. **32:** 228. 1951. Type: Fiji, Viti Levu, *A. C. Smith 5578* (A, holotype; K, isotype).

Lord Howe Island. "Section," Sept. 1853, *Milne* (K); Transit Hill, low dryish forest, 13 Nov. 1963, *P. S. Green 1615* (A, K) & *1617* (A, K); Erskine Valley, on lower part of ascent of Mt. Gower, dry forest on very rocky ground, 14 Nov. 1963, *P. S. Green 1669* (A, K). Without precise locality, *C. Moore 9* & *36* (K).

Norfolk Island. [1773], *Forster* (BM, K, isotypes); shady woods, 1830, *A. Cunningham 4* & *147* (K); Apr. 1835, *Backhouse 659* (K); Nov. 1898, *Robinson* (BM); May 1904, *Robinson* (K).

New Hebrides. North central Eromanga, tableland covered with bracken, volcanic ash, 500 ft. [132 m.] alt., 5 Aug. 1930, *L. E. Cockayne 53* (K).

Fiji. Viti Levu: Nandronga & Navosa, northern portion of Rairaimatuku Plateau, between Nandrau and Nanga, alt. 725–825 m., in dense forest, 4–7 Aug. 1947, *A. C. Smith 5578* (A, holotype of *Fagara gillespieana*; K, isotype); summit ridge of Mt. Loma Langa, 21 Nov. 1927, *Gillespie 3943* (GH); Naitasiri (?), Colo-i-Suva, alt. 180 m., 19 May 1961, *I. Bola 35* (K). Fulanga: in forest on limestone formation, alt. 0–80 m., 22–26 Feb. 1934, *A. C. Smith 1150* (GH, K).

Tonga. Vava'u and Lifuka, Aug. & Oct. 1855, *Harvey* (K); Vava'u, Dec. 1891, *Crosby* (K, male & female); Vava'u, in forest near Leimata village, NW. of Neiafu, 19 May 1953, *Yuncker 16045* (GH).

More material of this species, from throughout its range, is needed for examination. It is apparent that variation occurs between the populations on the island groups, or at least between those on Lord Howe and Norfolk Islands, and perhaps the New Hebrides, and between these and Fiji and Tonga. The New Caledonian plant which has been treated as this species by some is described below as a separate, but closely related, species.

No material has been seen from Tahiti but it is suspected that *Zanthoxylum nadeaudii* Drake del Castillo, Ill. Fl. Ins. Mar. Pacif. 130. 1890 & Fl. Polynésie Franç. 24. 1893 (*Blackburnia pinnata* var. *tahitensis* Nadeaud, Enum. Pl. Indig. Ile Tahiti 75. 1873; *Fagara nadeaudii* (Drake) J. W. Moore, Bull. Bishop Mus. **226:** 7. 1963) is part of this species, too. Of the main differentiating characters cited by Drake del Castillo, the

less deeply divided calyx could certainly apply to the specimens seen from Fiji and Tonga, and the leaf shape probably falls into the range of variation for this species.

For each of the specimens cited above, and those which had been determined as this species from New Caledonia, I scored the lengths of the leaf rachis and leaflet, the texture and number of leaflets per leaf, the bud shape, the petal, filament and anther length, and the fruit dimensions. After analysis of the results I was tempted to separate three subspecies together with the new species from New Caledonia, but in view of the range of variation on each of the other islands additional and better material is required to assess more accurately the following trends and differences which were noted.

NORFOLK ISLAND (type locality). Here there is a tendency for fewer leaflets (4–6 per leaf, 5–8 in Lord Howe Island specimens).

LORD HOWE ISLAND. Two specimens, *Green 1617* & *1669* (both male) appear very different from any other except the New Hebridean specimen by virtue of a sinuate-serrate upper margin to the leaflets, an articulation in the middle of individual pedicels (not more or less at the base), a small calyx, slim filaments (more or less uniformly broad from base to apex, not broadest at the base and tapering upwards), and the large anthers (1.7–1.8 mm. long in contrast to 1–1.2 mm. elsewhere). However, *Moore 9* (also male) has flowers like the type plant and, together with *Moore 39* and *Green 1615* bears foliage resembling more closely the Norfolk Island plant.

NEW HEBRIDES. Unfortunately the only collection seen from these islands is a male specimen and therefore without fruit for comparison with the related New Caledonian species, but the leaves, buds, and flowers resemble the Lord Howe Island plants represented by *Green 1617* & *1669*, although slightly smaller in all parts.

FIJI & TONGA. Here there is a tendency for the texture of the leaf to be subcoriaceous, the leaflet number to increase, (6–)8–10(–15) per leaf, the calyx to be less deeply divided, and the petals to be longer (3.5–4.2 mm. long in contrast to 2.7–3.0 mm. elsewhere).

Fagara gillespieana was described by A. C. Smith from Fiji. I have examined the type, but the leaflet size and texture, upon which, to judge from the protologue, its differentiation seems mainly to have been based, can be matched elsewhere, and appear to me to fall within the range of variation for *Zanthoxylum pinnatum*.

Zanthoxylum pancheri *P. S. Green*, sp. nov., affine *Z. pinnato*, a quo foliis plerumque brevioribus magis coriaceis, alabastris conicis acuminatis, et praesertim fructibus minoribus differt.

Blackburnia pinnata sensu Pancher in Sebert & Pancher, Not. Bois. Nouv. Caléd. 244. [1874], *non* J. R. & G. Forst.

Zanthoxylum blackburnia sensu Guillaumin, Ann. Mus. Coll. Marseilles II. 9 (Cat. Pl. Phan. Nouv.-Caléd. 1: 39): 111. 1911, *non* Benth.

Fagara pinnata sensu Guillaumin, Fl. Nouv.-Caléd. 164. 1948, *non Blackburnia pinnata* J. R. & G. Forst.

Blackburnia pulchella Vieill. ex Guillaum. Ann. Mus. Col. Marseilles II. 9 (Cat. Pl. Phan. Nouv.-Caléd. 1: 39): 111. 1911, *nom. nud.* Type: New Caledonia, 1861–67, *Vieillard 2452* (GH, K, isotypes).

Zanthoxylum pinnatum sensu Däniker, Viert. Naturf. Ges. Zürich 77 (Beibl. 19): 195. 1932, *non Blackburnia pinnata* J. R. & G. Forst.

Evergreen *shrub or tree* to 10 m. high; branchlets glabrous or very minutely puberulous when young. *Leaves* pinnate or imparipinnate, glabrous; rachis canaliculate, glabrous or very minutely puberulous when young, (2.5–)4–7(–9) cm. long; petiolules canaliculate 2–4(–5) mm. long; leaflets (4–)6–8(–14) in opposite pairs, subcoriaceous, asymmetrically elliptic to ovate, the part on the adaxial side of the midrib much broader than that on the abaxial, (1.4–)1.8–4.5(–5.5) cm. long by (0.9–)1.2–2.4(–2.8) cm. broad; margin entire, slightly recurved; apex obtuse or bluntly and shortly acuminate; base obtuse or acute, adaxial part usually rounded, the abaxial narrowly acute; venation raised and more or less reticulate above and below. *Inflorescence* axillary, cymose, paniculate, (3–)4–8(–9) cm. long, very minutely puberulous. *Flowers* unisexual, 4-merous. *Calyx* synsepalous, lobes shallow or broadly triangular, 0.5–0.75 mm. long. *Corolla* valvate, more or less conical and bluntly acuminate in bud; petals lanceolate, 2–3 mm. long. *Stamens* antesepaline, filaments 1.2–1.5 mm. long; anthers 0.5–0.7 mm. long. *Ovary,* in male flowers narrowly conical, 1 mm. long, abortive; in female flowers ellipsoid, 1.8–2 mm. long, 1.2 mm. broad; style subapical, curved, 0.5 mm. long. *Fruit* more or less spherical, 1-seeded, bivalved capsule, 7–8 mm. long, 5–7 mm. broad; seed black, shiny.

New Caledonia. Without locality: "collines buisées," 1879, *Pancher s.n.* (holotype, K; isotype, BM); *Le Rat s.n.* (A). "In parva insula Jandé," *Vieillard 2451* (BM). Pum, 1861–67, *Deplanch 10* & *297* (A, GH, K). Mt. Poume, 1868–70, *Balansa 3137* (BM, K). Poume, frequent, less than 1000 ft. [308 m.] alt., scrub, 12 Dec. 1934, *Compton 2386* (BM). Montagne de Gomouen, près Gatope, 1861–67, *Vieillard 310* (GH, K). Collines de Gomouen, Gatope, 1861–67, *Vieillard 2452* (BM, GH, K). Oundjo, between Koné and Voh, alt. 0–100 m., 30 Mar. 1956, *McKee 4211* (A, K). Bourail, 1868–70, *Balansa 1170* (BM, K) & 29 Mar. 1869, *Balansa 1171* (A, BM, K). Tontouta Valley, steep rocky slope, N. side of valley at junction of Kaleouéhola, alt. 50–300 m., 15 July 1956, *McKee 4894* (K). Nouméa, 1868–70, *Balansa 433* & *1687* (BM, K). Nouméa (Ouen Toro), 1 May 1917, *Franc 2099* (A). Bois de Port-Despointes (Nouméa), "bois secs des collines littorales, schistes nummulitiques," 14 Nov. 1942, *Virot 820* (A).

After concluding that the New Caledonian plants which have passed under the name *Zanthoxylum pinnatum* constitute a distinct and undescribed species, it was interesting to discover that von Mueller had come to the same conclusion about a century ago (see Fragm. Phytogr. Austral. 7: 141. 1871). I have followed his suggestion in naming the species after the French collector and botanist J. Pancher.

Zanthoxylum pancheri is closely related to *Z. pinnatum*; the leaves are more coriaceous, although occasional specimens of the latter species from Fiji approach it in this character, also the leaves are generally

shorter and smaller. Most clearly, however, it is separable by the size of its fruit, 7–8 × 5–7 mm., as opposed to 10–12 × 7–10 mm. in *Z. pinnatum*. Furthermore, a good "spot" character when the flowers are in bud is the conical, somewhat acuminate, bud, in contrast to an obtuse, rounded bud in the other species.

VIOLACEAE

The nomenclature of the shrubby members of this family on Norfolk and Lord Howe Islands has been remarkably confused, but a comparison of specimens from these islands with material from New Zealand, Australia, and other Pacific areas has shown that three separate taxa are worthy of recognition. Beuzenberg (1961) has shown that the genera *Melicytus* J. R. & G. Forst. and *Hymenanthera* R. Br. should be united and, following him, the three taxa are placed in the genus *Melicytus*.

Melicytus latifolius (Endl.) P. S. Green, comb. nov.

Hymenanthera latifolia Endl. Prodr. Fl. Norfolk. 70. 1833 & Ic. Gen. Pl. xiii. *t. 108*. 1840; Tate in Fletcher, Macleay Mem. Vol., Linn. Soc. New S. Wales 215. 1893; Kirk, Trans. & Proc. New Zealand Inst. **28**: 514. 1896; Maiden, Proc. Linn. Soc. New S. Wales **28**: 696. 1903; Hemsley, Bull. Misc. Inf. Kew **1908**: 95. 1908; Laing, Trans. & Proc. New Zealand Inst. **47**: 32. 1915; Hoogland in Turner *et al.* Austral. Conservation Foundation Spec. Publ. **1** (The Conservation of Norfolk Is.): 35. 1968.

Suttonia ? *tenuifolia* Hook. f. Fl. Antarct. **1**: 52. 1844; Mez in Engler, Pflanzenreich IV. **236** (Heft 9): 335. 1902.

Norfolk Island. Without precise locality: *Bauer* (K, isotype), *Caley* (A) & April 1835, *Backhouse 628* (K); skirts of woods, July 1830, *A. Cunningham 43* (holotype of *Suttonia tenuifolia*, K). Upper slopes of Mt. Pitt, 1937 & 1939, *McComish 45* (A, K).

The exact identity of Hooker's *Suttonia tenuifolia* has been held in some doubt; Laing in his list of Norfolk Island plants (Laing, 1915) says he knows nothing of it and Mez in his monograph of the *Myrsinaceae* in Engler's Pflanzenreich places it as a "species dubia." However, the type specimen, with the name in Hooker's hand, had, to judge from the pencil annotations upon it, been early recognized as not belonging to the *Myrsinaceae* and marked "cfr. *Melicytus*" and "cfr. *Hymenanthera*," where it was found in the Kew herbarium.

In November 1937, Capt. J. D. McComish noted that he had only found one tree of *Melicytus latifolius* and that he had "made a thorough search, but cannot find another." However, in 1939 he said that he has "now found several other trees but none as large as the original." Turner, Smithers & Hoogland in their excellent report on "The Conservation of Norfolk Island" p. 35, say "A small tree, fairly common in the forests of Mt. Pitt Reserve, in particular at the higher levels." However, there may be some confusion with *M. ramiflorus* subsp. *oblongifolius*, see below.

Melicytus novae-zelandiae (A. Cunn.) P. S. Green, comb. nov.

Scaevola ? novae-zelandiae A. Cunn. Ann. Mag. Nat. Hist. **2:** 52. 1839. Type: New Zealand, North Island, at Matauri, on the sea coast opposite the Cavallos Isles, 1834, *R. Cunningham [429]* (K).

Hymenanthera novae-zelandiae (A. Cunn.) Hemsley, Bull. Misc. Inf. Kew **1908:** 96. 1908; Allan, Fl. New Zeal. **1:** 194. 1961.

Subsp. **centurionis** P. S. Green, subsp. nov., a subsp. *novae-zelandiae* foliis chartaceis angustioribus, caulibus junioribus minute papilloso-puberulis differt.

Hymenanthera latifolia sensu Hemsley, Ann. Bot. **10:** 231. 1896, *non* Endl.

H. novae-zelandiae sensu W. R. B. Oliver, Trans. & Proc. New Zealand Inst. **49:** 143. 1917, *non* (A. Cunn.) Hemsl.

Shrub to 2.5 m. high with many stems; branches spreading, glabrous or very minutely papillose-puberulent when young. *Leaves* chartaceous; petioles 2–5 mm. long; lamina oblanceolate-elliptic, (3.5–)4–7 cm. long, (1.2–)1.5–2.7 cm. broad; base narrowly cuneate and decurrent onto the petiole; apex acute or obtuse and rounded; margin crenate-serrate with (3–)5–6(–8) teeth per side, not thickened or recurved; veins raised and reticulate above and below, (4–)5–6(–7) primary veins per side. *Inflorescence* axillary to old leaves or their petiole scars with 1 or 2 fasciculate dioecious flowers; pedicels 1.5–2 mm. long with, in the middle, 2 opposite bracts with erose rounded margins. *Calyx* of 5 imbricate, erose, rounded lobes about 1 mm. long and 1–1.2 mm. broad. *Corolla* of 5 lanceolate rounded lobes 2.5–4 mm. long (the smaller in the ♀) more or less reflexed at their tips. *Stamens* 5, connate by a dorsal membrane produced laterally and above the anthers into 5 more or less lanceolate lobes 2 mm. long, slightly curled at the apex and erose-fimbriate; anthers 1 mm. long with a more or less cuneiform nectariferous sac borne dorsally 0.6 mm. long. *Ovary* elongated ovoid 2.5 mm. long, contracted into a very short style with 2 somewhat recurved stigmatic lobes. *Fruit* globose, (?) a berry, about 5 mm. in diameter, with a persistent style.

Lord Howe Island. "Apparently scarce, as I have only seen 4 plants," 15 Nov. 1938, *McComish 166* (holotype, K); Dawson's Point, *Eclipse Expedition, C. Moore 64* (K); without precise locality, *Fullager* (K).

Although previously treated as the New Zealand plant, this subspecies is quite distinct. Not only are the leaves much thinner in texture and narrower in proportion to their length, giving them a more narrowly cuneate base, but the margins are not, or scarcely, thickened and recurved. In addition the young stems and bases of the petioles when examined through a strong lens are found to be papillose-puberulent and not glabrous as in the New Zealand plant. Any floral differences that exist are small and it is clear that separation at the rank of species is scarcely justified.

It is a pleasure to name this plant in honor of Captain J. D. McComish who, in a letter to the Director of the Royal Botanic Gardens, Kew,

wrote on 9th November 1946, "I am convinced that this plant is not identical with the New Zealand plant and Dr. Oliver agrees with me in this. However, all the plants, so far as I know, bear only pistillate flowers, but I have a man searching the Island for plants with staminate flowers." Whether any were found I do not know but we may hope that staminate plants exist and that this subspecies, which must be very rare, does not become extinct. The plant from which the Fullager collection cited above came, bore male flowers.

Melicytus ramiflorus J. R. & G. Forst.
Subsp. **oblongifolius** (A. Cunn.) P. S. Green, stat. & comb. nov.

Hymenanthera oblongifolia A. Cunn. Hook. Lond. Jour. Bot. **1**: 124. 1842.
Melicytus ramiflorus sensu Hook. f. Handb. New Zealand Fl. 17. 1867, *pro parte*; F. Muell. Jour. Bot. **23**: 354. 1885; C. Moore & Betche, Handb. Fl. New S. Wales 518. 1893; Maiden, Proc. Linn. Soc. New S. Wales **28**: 697. 1903; Laing, Trans. & Proc. New Zealand Inst. **47**: 32. 1915, *non* J. R. & G. Forst.
Hymenanthera dentata R. Br. var. *oblongifolia* (A. Cunn.) Kirk, Trans. & Proc. New Zealand Inst. **28**: 511. 1896.

Norfolk Island. June-July 1830, *A. Cunningham 44* (K); "on the skirts of woods, at Long Ridge, at the junction of the old cross road leading to Cascade Road," July 1830, *A. Cunningham 42* (*127**) (holotype, K); April 1835, *Backhouse 641* (K); woods, June 1855, *Milne 4* (K).

No recent collections of this plant have been seen but Laing (1915) says that it is "not uncommon in the bush." It is to be hoped that it is protected from extinction.

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ROYAL BOTANIC GARDENS
KEW, RICHMOND, SURREY
ENGLAND

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 12. A NEW SPECIES OF GONOCALYX (ERICACEAE).

Lorin I. Nevling, Jr.

During the course of an ecological study of an elfin forest situated on Pico del Oeste, Sierra de Luquillo, Puerto Rico, a similar but not identical area, Cerro La Santa in the Bosque Estatal de Guavate-Carite, was visited and observed for comparative purposes.[1] The Cerro La Santa site is situated approximately 25 miles southwest of Pico del Oeste at a slightly lower altitude (903 m.) and has a lower annual rainfall. Surprisingly, the component genera of the two forests are very similar: some species are common to both, but in some genera different species are found. Two most interesting ericaceous plants belonging to the latter category are *Gonocalyx portoricensis* (Urb.) A. C. Smith from the Sierra de Luquillo and an undescribed species of the genus from Cerro La Santa. The purpose of this note is to describe the new species and to comment on certain aspects of the typification and date of publication of the genus.

With the addition of *Gonocalyx concolor* the genus comprises four species: one from Colombia (the type species); one from Dominica; and two from Puerto Rico. There are, in addition, two collections which may represent still other species belonging to this genus. In 1945, A. C. Smith annotated a specimen in the Gray Herbarium as follows, "Cuatrecasas 17184 represents an undescribed species, probably referable to *Gonocalyx*. Only one flower is available and the specimen does not seem ample enough for description." The specimen bears the following data, "Colombia, Departamento del Valle, Costa del Pacífico; río Cajambre; Barco, 5–80 met. alt. 21–30 abril 1944." The plant is an epiphytic shrub with carmine flowers and narrowly elliptic leaves. Smith may be correct in his placement of this entity but over-fractionation of genera in the Thibaudieae (or Vaccinioideae) makes intercalation of new material very difficult. Another collection, our specimen is sterile, which may belong to *Gonocalyx* is *Idrobo & Schultes 961*. "Colombia: Meta: Cordillera La Macarena (extremo nordeste) macizo Renjifo, cumbre y alrededores. alt. 1.300–1.900 m. Enero 6–20, 1951." The plant is epiphytic with a white corolla and leaves somewhat reminiscent in size and shape of those of *G. portoricensis*.

[1] The field work which led to this note was supported by a grant from the National Science Foundation (GB: 3975) to Dr. Richard A. Howard with whom I spent many instructive hours in the field. Special thanks are due Dr. Howard Pfeifer for locating and photographing certain critical specimens and notes while at Kew. Thanks are due Mr. R. Desmond, Librarian at Kew, for arranging the photocopying of critical text and to Dr. L. Emberger of Montpellier for the gift of a photograph of the type of *Gonocalyx pulcher*. The line illustration of the anthers is the work of Miss Pamela Bruns. I am also grateful to Mr. Joseph B. Martinson for providing facilities and generous hospitality in Puerto Rico.

Considerable emphasis has been placed upon the length of the corolla tube and the anther tubules in delimiting the genus *Gonocalyx* (see A. C. Smith, The American Species of Thibaudieae. Contrib. U. S. Natl. Herb. 28: 311–547. 1932, and H. Sleumer, Vaccinioideen-Studien. Bot. Jahrb. 71: 375–510. 1941). As a result of this approach, the genus may be composed of species which are not necessarily closely related (except for *G. portoricensis* and *G. concolor*). It is possible, if not probable, that the increase in length of corolla tube and anther tubules is the result of selection for specific pollinators and that this selection has occurred independently in Colombia, Dominica, and Puerto Rico. Each corolla segment is innervated by three main veins: a median and two laterals. The laterals depart from the main vein at the very base of the corolla tube. Further, the laterals do not fuse with those of the adjacent corolla lobes, a condition which I believe indicates "incomplete" fusion and one which may permit greater flexibility in modifying tube length. It does not appear that length of corolla tube and length of anther tubule are correlated i.e., the longer the tube the longer the tubules. On the contrary, it seems that in *Gonocalyx* the increase in length of corolla tube is a secondary and derived development and should not be considered of primary taxonomic importance in generic delimitation.

Key to the Species of Gonocalyx

A. Leaves elliptic, ovate, or orbicular, 0.5–3 cm. long, the apex obtuse, retuse, or acute and apiculate; flowers borne singly or in pairs in the leaf axils; anther tubules 8–11 mm. long.
  B. Leaf margin entire or inconspicuously crenate; corolla tube 12–16 mm. long. Plants of Puerto Rico.
    C. Leaf margin usually strongly revolute; calyx light green; corolla tubular, pink or rose fading to white at the apex, the corolla lobes erect; stigma at most subexserted at anthesis, white. ..... *G. portoricensis.*
    C. Leaf margin plane; calyx red; corolla campanulate, uniformly red, the corolla lobes spreading; stigma exserted at anthesis, red. ..... *G. concolor.*
  B. Leaf margin shallowly but conspicuously crenate at least towards the apex; corolla rose, fading to white at the apex, tube ca. 20 mm. long. Plants of Colombia. ..... *G. pulcher.*
A. Leaves ovate, 6–10 cm. long, the apex acuminate; inflorescence loosely racemose, axillary, 3–8-flowered; corolla red; anther tubules ca. 3.5 mm. long. Plants of Dominica. ..... *G. smilacifolius.*

Gonocalyx concolor Nevl., sp. nov.

Frutex sempervirens epiphyticus parvus, irregulariter ramosus. Ramuli velutini rhodochroi. Folia petiolata ovata elliptica vel orbiculata 1.5–3 cm. longa 1.5–2.25 cm. lata ± integerrima coriacea rigida plana apice acuta vel rotundata brevissime apiculata basi rotundata superficie glabra infra pilis sparsim instructa, nervo medio supra impresso, subtus prominenti. Inflorescentia lateralis uniflora. Calyx obprismaticus 3–3.5 mm.

longus ruber glaber. Corolla campanulata 13–15 mm. longa 6–7 mm. in diametro ruberis lobis patentibus 2–3 mm. longis 4 mm. latis. Stamina 10 aequilonga exserta antheris ca. 3 mm. longis apiculatis tubulis ca. 10–11 mm. longis, filamentis liguliformibus ca. 2 mm. longis. Ovarium 5-loculare, ovulis pluribus. Stylus filiformis ruber; stigma minutum. Baccae non visae.

Holotypus: *Howard & Nevling 16947* (A).

Small epiphytic shrubs, evergreen, the young branches and leaves rose-colored, minutely velutinous and glabrescent. Leaves simple, alternate, coriaceous, the blade ovate, broadly elliptic, or nearly orbicular, 1.5–3 cm. long, 1.5–2.25 cm. broad, apiculate and obtuse to acute at the apex, rounded at the base, glabrous above, with a few large trichomes beneath, the venation 5-pli from the base, outer set marginal, inner set submarginal and better developed, the midvein immersed above, emersed beneath, the margin entire except for a few inconspicuous crenations toward the apex; petiole to 2.5 mm. long, velutinous, young leaves brilliantly rose-colored becoming green. Flowers bisexual, 5-merous, regular, uniformly vivid red (Nickerson 5R 5/13), borne singly on axillary brachyblasts, semipendent; pedicel terete, 9–11 mm. long, red, fringed with trichomes at the summit, bibracteolate near the base, articulated with the calyx; calyx tube obprismatic, 3–3.5 mm. long, conspicuously 5-ribbed, ribs alternisepalous, red, glabrous, the lobes very broad and apiculate, the calyx limb margin nearly entire; corolla tube campanulate, 13–15 mm. long, 6–7 mm. in diameter, carnose, with a few multicellular trichomes mostly below the middle, glabrous within, deciduous, the lobes 5, 2–3 mm. long, 4 mm. broad, spreading; stamens 10, equal, free, inserted on a fleshy 10-lobed disc, deciduous, the anther sacs granular, ca. 3 mm. long, apiculately appendaged, pollen in tetrads, the tubules ca. 10–11 mm. long, opening by introrse elliptical pores 0.5–0.75 mm. long, apices exserted, the filaments liguliform, pubescent on margins, ca. 2 mm. long; ovary inferior, 5-carpellate and -loculate, the placentation axile, ovules many, the style filiform, vivid red, glabrous, persistent, the stigma truncate, exserted at anthesis. Berry not seen.

Specimens examined: **Puerto Rico.** Bosque Estatal de Guavate-Carite, Cerro La Santa, *Howard & Nevling 16947* (A, holotype; isotypes to be distributed), *Howard 17255* (A), *Wagner & Wagner*, April 27, 1968 (A), *Bro. Alain Liogier 10405* (GH, NY).

There is little question that *Gonocalyx portoricensis* and *G. concolor* are derived from common ancestral stock. There is great similarity in many details and in aspect, as well as geographic proximity. The differences which have developed are due, in my opinion, to a divergence in the pollinators. The flower of *G. portoricensis* is pendent with a light green calyx and a corolla tube which is pink or rose at the base fading to white at the orifice. The filaments have inwardly and laterally directed trichomes protecting a green, glandular base. It is most likely that it

FIGURE 1. Photograph of *Gonocalyx concolor* (*Howard & Nevling 16947*) in nature, approximately twice natural size.

is insect pollinated although it must be pointed out that this species was under observation on Pico del Oeste for a period of two years and no pollinators were observed. It is in flower sporadically throughout the year and seems to set fruit regularly. The flower buds are sometimes parasitized by an unidentified insect larva which eats the anther sacs and pollen. The newly described *G. concolor* differs, in part, by having the flowers semipendent (borne at about 45° from the vertical), with vivid red calyx, corolla, and stigma. In addition, the corolla tube is campanulate with the lobes spreading (see FIGURE 1). Slight differences are also noted in the details of the anthers (FIGURE 2). It is possible and purely speculative, for no pollinator has been observed here either, that this species has diverged towards hummingbird pollination. It has been collected in flower in December, January, February, and April and doubtless has a much longer flowering period.

A problem which came to my attention during the preparation of this note was an apparent discrepancy in the date of publication of *Gonocalyx pulcher*. There are several publications of 1856 which must be considered in some detail to resolve the matter. These are presented in presumed chronological order for discussion.

1. GARDENERS' CHRONICLE **1856**: 152. (March 8) 1856.

Under the title "New Plants" is listed "164. GONOCALYX PULCHER *Planchon and Linden Fl. Columb. ined.* We have received from Mr. Linden a coloured representation of this pretty plant which he offers for sale at 25 fr., and of which we translate his description." The descrip-

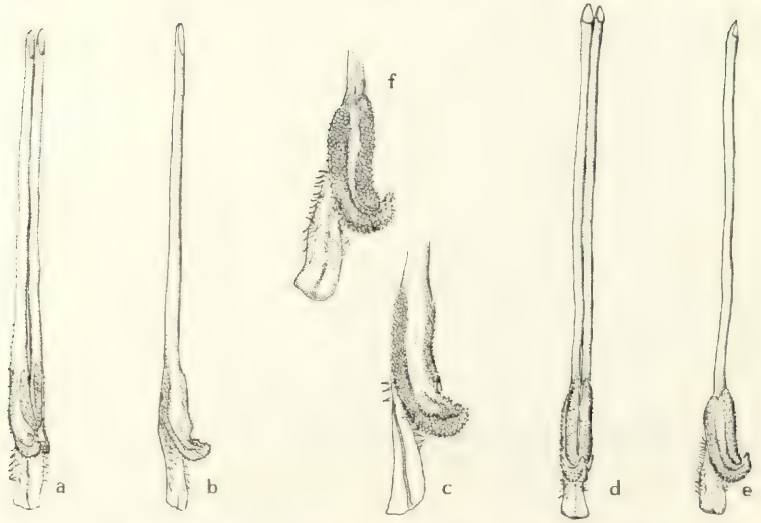

FIGURE 2. Stamens of *Gonocalyx portoricensis* and *G. concolor*. a–c, *G. portoricensis*; a, stamen, adaxial view, × 4; b, stamen, lateral view with only one tubule shown, × 4; c, filament and anther sac, lateral view, × 6; d–f, *G. concolor*; d, stamen, adaxial view, × 4; e, stamen, lateral view with only one tubule shown, × 4; f, filament and anther sac, lateral view, × 6.

tion follows and is accompanied by a black and white illustration of a single flowering branchlet.

This publication is cited in *Index Kewensis* (Vol. 2) as the place of publication of *Gonocalyx*, an opinion which was accepted by two specialists in American Ericaceae, A. C. Smith and H. Sleumer. The *Index Nominum Genericorum* lists the generic authority as Planchon et Linden ex Lindley, while Supplement 13 of *Index Kewensis* has an entry attributing the genus to Planchon & Linden ex A. C. Smith!

2. FLORICULTURAL CABINET **24**: 57. (March) 1856.

Two plants, *Cuphea eminens* and *Gonocalyx pulcher*, are described in English, each in a separate paragraph. Each description is chatty in nature and presents some of the information included in *Gardeners' Chronicle* plus a few notes on horticulture. Some errors have been introduced including the notation that the *Gonocalyx* is from Ocana, Mexico. A colored plate illustrates a flowering branch of each species.

3. BELGIQUE HORTICOLE **6**: 231, 232. 1856.

In a section entitled "Plantes nouvelles de serre froide et tempérée." and subtitled, "Mises pour la première fois dans le commerce, par *M.* J. Linden" five species are listed: *Calyptraria haemantha*, *Cuphea eminens*, *Monochaetum ensiferum*, *Gonocalyx pulcher*, and *Scutellaria trianaei*. Preceding the descriptions is a notation "Extrait du catalogue de *M.* Linden,

pour 1856." The text is nearly a faithful reproduction of the *Catalogue* presentation. There are no illustrations.

4. REVUE HORTICOLE IV. **5**: 162–165. 1856.

In an article by Ch. Martins entitled "Revue de l'Horticulture étrangère" is a description of *Gonocalyx pulcher* which was taken from the *Gardeners' Chronicle*. The description is a French translation of the English translation.

It would appear that no one seriously considered the possibility of valid publication of *Gonocalyx* in Linden's *Catalogue* of 1855. It is absolutely clear that Linden supplied the text and illustration to *Gardeners' Chronicle* with the intent of publicizing his new plant. The *Floricultural Cabinet* of the same month indicates that the plants are available through Mr. Linden's London agent. We suspect that there was a bit of promotion on Mr. Linden's part and that the source of information and of the illustration in the *Cabinet* was the *Gardeners' Chronicle*. The two remaining publications of 1856 are clearly repetitions or translations of previous publications. Corroborative evidence indicating that this interpretation is correct is to be found in the nature of the illustrations. The *Catalogue* contains a fine colored plate which includes three flowering branches and several vegetative ones. The plate in the *Chronicle* is the left-hand flowering branchlet from the *Catalogue* printed without color and in reverse. The illustration in the *Cabinet* is the central flowering branchlet from the *Catalogue*. The complete (and original) plate which appears in the *Catalogue* was, in my opinion, originally prepared for publication in the Belgian periodical *Flore des Serres*, but never used there. All facts lead to the conclusion that Linden's *Catalogue* of 1855 did precede all the 1856 publications and should be considered the place of valid publication for *Gonocalyx pulcher*. I believe the description (Catalogue (Prix-courant de l'établissement d'introduction pour les plantes nouvelles) p. 5, 6. 1855) should be interpreted as a combined generic-specific description and that priority of *Gonocalyx* was established at that time. Indirect evidence (i.e., the title page lists "Printemps, Été et Automne de 1855) may point to publication late in the year.

A parallel problem with that of publication is that of typification. A. C. Smith typified *Gonocalyx pulcher*, the type species, by a specimen grown and deposited at Kew (specimen collected in October 1879). This sheet bears the *Gardeners' Chronicle* reference and it is possible, if not probable, that the specimen had its origin from Linden's original sale offering. The important questions are when, where, and by whom the original gathering was made. On the basis of the information supplied by Linden, the original discovery was made by Schlim (Linden's half-brother) "en compagnie du *Calyptratia haemantha*, etc., dans les provinces de Pamplona et d'Ocaña." According to Linden, *Calyptraria* was discovered in 1844 by Schlim at the Paramo de Cachiri and was later found also at Ocaña.

It is of interest that other sources [2] place Schlim with Linden from the beginning of 1844 (exploring the Santa Marta) until 4 March when they sailed for Europe. Coincidentally, Planchon sets the date of discovery of *C. haemantha* as 1847 (Flore des Serres 9: 171, 172, *pl. 924.* 1854). In October of 1845 Funck and Schlim returned to South America and began exploration and plant collection on behalf of Linden. They collected around Pamplona, Chinácota (and Ocaña?) until Funck departed in 1847 with the plant shipment for Europe. Perhaps it is to this date of introduction for *Calyptraria* and not to the date of actual discovery to which Planchon refers. Linden stated that Schlim collected seeds and plants of the *Calyptraria* from the Ocaña site and that these were the origin of the plants which he offered for sale. It is possible that it was at this time that the *Gonocalyx* specimens were collected. However, Schlim remained in Colombia following Funck's departure and continued to collect in the vicinity of Pamplona (all specimens lost by shipwreck) and then near Ocaña. He returned to Europe in August of 1852. I believe it is clear that the *Gonocalyx* was not collected in 1844 but sometime between 1845 and 1852. If, indeed, Schlim was the sole collector the date is narrowed to the 1847–52 period.

Perhaps a more significant point is the role played by Planchon in this instance. Planchon collaborated with Linden and it was he who did the technical botanical aspects of their joint efforts. Planchon was at Ghent from 1849 to 1851, at Nancy from 1851 to 1853, and arrived in Montpellier in 1853. Linden would have sought Planchon's critical opinion prior to any decision to publish, particularly with such an interesting plant in a difficult family. A specimen, deposited at Montpellier, of *Gonocalyx pulcher* bears the printed label of J. Linden for the "Voyage de *L. Schlim.*" The geographic data (Ocaña) correspond to expectations. The date is given as 1851 and the collection number is 153; further, the notation "(vivant)" is included on the label. In addition, there are critical notes on the flower morphology. It is apparent that the *Schlim 153* (MPU) is the holotype (photo A) of *G. pulcher* Planchon & Linden and that Smith's typification was in error.

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[2] E. P. Killip. Report of the Killip-Smith botanical expedition to Colombia, 1926–1927. Jour. N. Y. Bot. Gard. **28:** 205–220, see especially footnote 3. 1927.

ANALYSIS OF THE COMPLEX VASCULARITY IN STEMS OF DIOSCOREA COMPOSITA

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PLANT ANATOMISTS HAVE, for many years, been presented with various diagrams designed to represent the course of vascular bundles in monocotyledons. In a comprehensive study Bary (1884) classified the vas-

FIGURES 1 and 2. Habit of *Dioscorea composita* Hemsl., × 1/2. 1. Male inflorescence.

cular systems of the monocotyledons into three main categories viz., the palm type, the type of the Commelinaceae, and that of the "anomalous monocotyledons," i.e. those "which differ fundamentally from . . . the very great majority of Monocotyledons."

In spite of some variation in the vascular tissue in stems of the palm type, the salient features of this construction are similar. Leaf trace bundles are present in all stems together with main vascular stem bundles. The main vascular bundles have the tendency to run near the periphery of the stem axis and nearly parallel with it. A large number of bundles from each leaf enter the stem separately and take a radially oblique course. In large plants such as the palms the number of bundles reaches several hundred. The bundles from different parts of the same leaf penetrate

2. Female inflorescence.

the stem to different depths. The midvein penetrates deepest, while those of the margins extend the least distance.

The stem type of the Commelinaceae was described as similar to the dicotyledonous arrangement of tissues. The stem bundles occur in a circle lying near the periphery. These are some distance from the leaf trace bundles which are near the center.

The so-called anomalous type of stem, including that of the Dioscoreaceae, was described as nearest to that of the dicotyledons in its vascular system. The leaf traces are arranged in a single circle around the circumference of the central cylinder. The vascular bundles penetrate radially into the stem center, extending to unequal depths.

In an early study of the stem of the Dioscoreaceae Mohl (1845) made a comparison with the stem of the Palmae. He concluded that the vascular architecture of these two families was similar although there were some peculiar histological details in the Dioscoreaceae.

Zimmermann and Tomlinson, in a series of articles on the anatomy of the palm *Rhapis excelsa* and *Prionium* (Juncaceae) (Zimmermann & Tomlinson, 1965, 1967, 1968; Tomlinson & Zimmermann, 1966a, 1966b, 1968a, 1968b), have made some very revealing studies showing more accurately than had previously been done the pathway of the vascular bundles. The studies of *Rhapis excelsa, inter alia,* are intended to serve as a model to represent (a) the course of vascular bundles including (1) leaf trace; (2) vertical bundles; (3) bridge bundles and (4) satellite bundles; (b) the dynamic flexibility that enables some monocotyledons to produce variable numbers of vascular bundles; and (c) the fact that there is no continuity of metaxylem between the stem and the leaf, hence, the leaf is irrigated solely by protoxylem.

In a recent publication (Ayensu, 1969), an attempt, based on the conventional technique, was made to summarize and explain how the vascular tissue of two successive internodes maintains continuity in the complex nodal structure in stems of the Dioscoreaceae. It became evident that a more reliable understanding of the pathway in the vascular system would be gained by the use of the motion picture analysis technique.

Four species of the Dioscoreaceae (*Dioscorea composita* Hemsl., *D. polygonoides* Humb. & Bonpl., *D. friedrichsthalii* R. Knuth and *Tamus communis* L.) have so far been analysed by the Optical Shuttle method. *Dioscorea composita* has been selected to illustrate here the pathways observed in the species listed.

MATERIALS AND METHODS

Dioscorea composita (FIGURES 1, 2) is a vigorously growing climber with a glabrous, cylindrical, woody stem. The vine has a tendency to become sulcate when dry. The leaves are alternate, simple, and with entire margins. The leaf blade is coriaceous, broadly ovate, cordate at base, abruptly acute at apex, or sometimes with the apex obtuse or apiculate.

The leaves are 10–25 cm. long and 5–20 cm. wide with 7–9 veins prominent on both surfaces. Petioles are 6–12 cm. long, sulcate and rather firm. The male inflorescence is prominent, 1–2 in the axils, compound, 20–30 cm. long, and with rachis slightly tomentose. Flowers lack pedicels, are 1–2–3-agglomerate, and occur about 2–3 mm. apart. Bracts are acute, and broadly lanceolate. The perianth is fleshy, tubular, slightly tomentose, and about 3 mm. long; its segments are ovate-orbicular, obtuse and erect, and almost the same length as the tube. The fertile stamens are 6, central, and erect; the filaments averaging 2 mm. long are unequal and fleshy. The style is rudimentary but conspicuous. The female inflorescence is elongate, simple or compound; the capsules are ovoid-oblong, 1.5–2.5 cm. long. The tubers are large, long, and penetrate deeply into the soil.

From the seeds sent me by Dr. Franklin W. Martin, plant geneticist, U.S. Department of Agriculture, Mayaguez, Puerto Rico, I was able to obtain germinated seeds of *Dioscorea composita* in petri dishes at 80° F, in ten days. Between two and three months later the vines were harvested for histological studies. Other material used for this study was collected by me during a visit to Puerto Rico. A herbarium specimen of *D. composita* (*Baldwin, 14238*), collected in Vera Cruz, was also revived (cf. Ayensu, 1967) and used for this study.

Material previously stored in the fixative FAA was washed thoroughly in running water for one hour. The stem pieces were then removed from the running water and passed through a series of alcohol concentrations from 50 percent to absolute. From the absolute alcohol the stem pieces were processed through the following changes:

1) 2/3 abs. alcohol and 1/3 chloroform
2) 1/2 abs. alcohol and 1/2 chloroform
3) 1/3 abs. alcohol and 2/3 chloroform
4) 2 changes of pure chloroform
5) 2/3 chloroform and 1/3 paraffin
6) 1/2 chloroform and 1/2 paraffin
7) 1/3 chloroform and 2/3 paraffin
8) 2 changes of paraplast

These alcohol-chloroform-paraffin/paraplast changes were conducted in an oven at intervals of 30 minutes.

Paraplast blocks containing the stems were cut at 10μ, on a rotary microtome. Each section was cut and mounted on a separate slide. Sections were numbered sequentially to facilitate the cinematographic analysis. The sections were dewaxed, stained with a mixture of safranin (95 parts of 1 percent solution in 70 percent ethanol) and Delafield's haematoxylin (5 parts), dehydrated, and mounted in Canada balsam.

The serial analysis of the sections was accomplished with the aid of the optical shuttle system (cf. Zimmermann & Tomlinson, 1965, 1966, 1968) consisting of two identical microscopes, discussion and image overlap tube (Zimmermann Adapter), and a 16 mm. movie camera. A Data Analyser Projector was used in the study of the films.

OBSERVATIONS

Anatomy of mature aërial stem. The paragraph which follows is a

summary of the description of the internode encountered in *Dioscorea composita*.

Trichomes absent; glands and stomata present. Cuticle thick and ridged. Epidermis composed of thick-walled circular or dome-shaped cells with cytoplasmic contents. Cortex of 6 to 10 layers of cells of variable size; 1–3 outer layers collenchymatous. Endodermoid layer separating cortex from 2 to 3 layers of fibers. Both common and cauline vascular bundles present. Common bundles V-shaped with one phloem unit at converging ends of the V, and two phloem units terminating the flanges of the V. Cauline bundles elliptical with one pair of large vessels each of average diameter of 430μ, and with one large phloem unit on inner side of innermost pair of large vessels close to the center of the pith, and another phloem unit at the outer end. Average diameter of large sieve tubes 96μ. Pith area constituting one fourth of central cylinder. Crystals: idioblast-containing raphide bundles with cuboidal crystals are also present. Tannin cells observed. Extra floral glands present.

Course of the vascular bundles. Internodes from the middle portion of the plant show the following progression: (1) Starting from the base upwards in an internode, it is observed that 8 common and 8 cauline vascular bundles maintain their strict individuality, as well as their shape, until about 850μ before a connection is made with the nodal region. At this point alteration occurs in the two, or in some special cases in the four, cauline vascular bundles facing the direction of the leaf insertion. The large phloem units on the inner side of the innermost pairs of metaxylem vessels begin to break down and anastomose (FIGURES 4, 5). (2) About 1550μ from above the innermost protoxylem elements of the same cauline bundles begin to anastomose. (3) This is followed by the fusion of the phloem elements from the two or four cauline bundles into a full manifestation of a phloem glomerulus. (4) Next is the development of the xylem glomerulus (FIGURE 6). (5) Following (3) and (4), the phloem units and the xylem elements of the common vascular bundles begin to anastomose into xylem and phloem glomeruli (FIGURE 7). (6) The large metaxylem vessels, until now not affected by the structural changes in the cauline vascular bundles, begin to lose their identity by merging into the xylem glomerulus (FIGURES 8–10). (7) The more centrally located phloem glomerulus "moves" radially between the remnants of the two adjacent cauline bundles and joins the outer one towards the glomerulus of the common bundle organized in the same radial direction. (8) The glomeruli of the other common bundles "move" in the direction of the point of the petiole insertion during the movement of (7). (9) The xylem glomerulus formed within the cauline bundles "follows" rapidly behind the phloem glomerulus described in (8), thereby completing the breakdown and the incorporation of the large metaxylem vessels into the plexus. (10) The phloem units at the outer end of the cauline vascular bundles are unaffected by the processes of anastomosis occurring in the node. Instead, the position of the phloem unit is altered only slightly by the stresses applied as a result of the outward "movement" of the xylem and phloem glomeruli. (11) At about the time that the outward "movement" of the glomeruli is completed, the reorganization of the tissues of the inner side of the cauline bundles begins. This reorganization is rapidly followed by the return of the outer half of the cauline bundle into its original position. At this point the elliptical shape of the bundles observed in transverse sections at the internode and in the petiole is restored (FIGURES 11, 12). (12) The reorganization of the common bundles follows the process described for (11). (13) At 12,480μ above the node

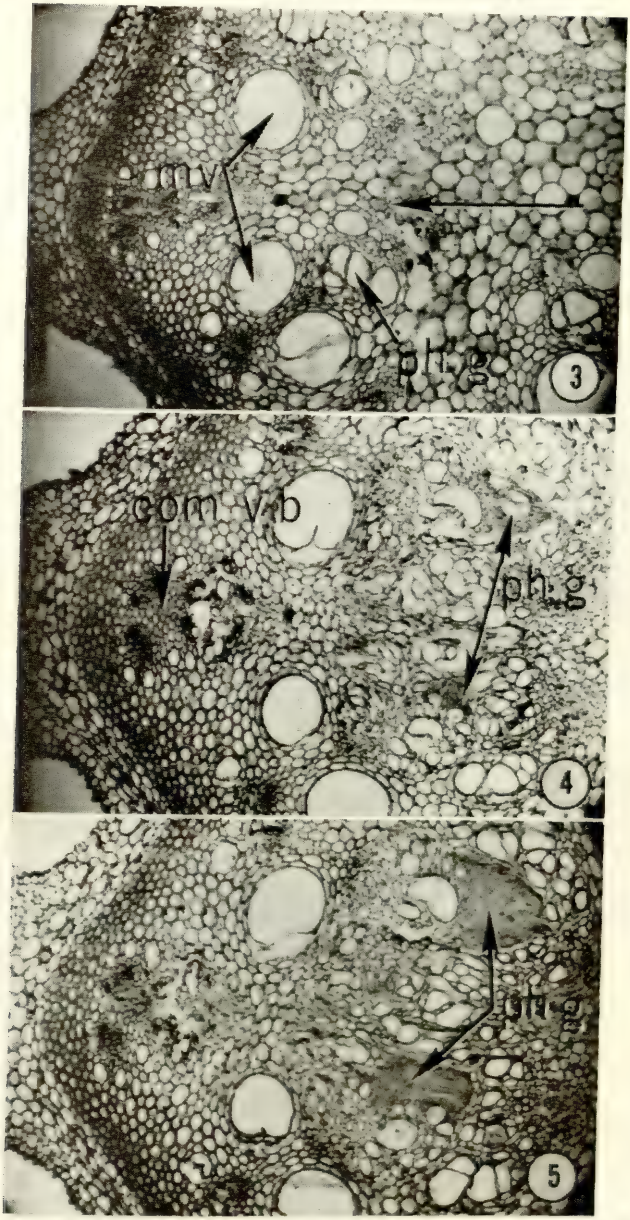
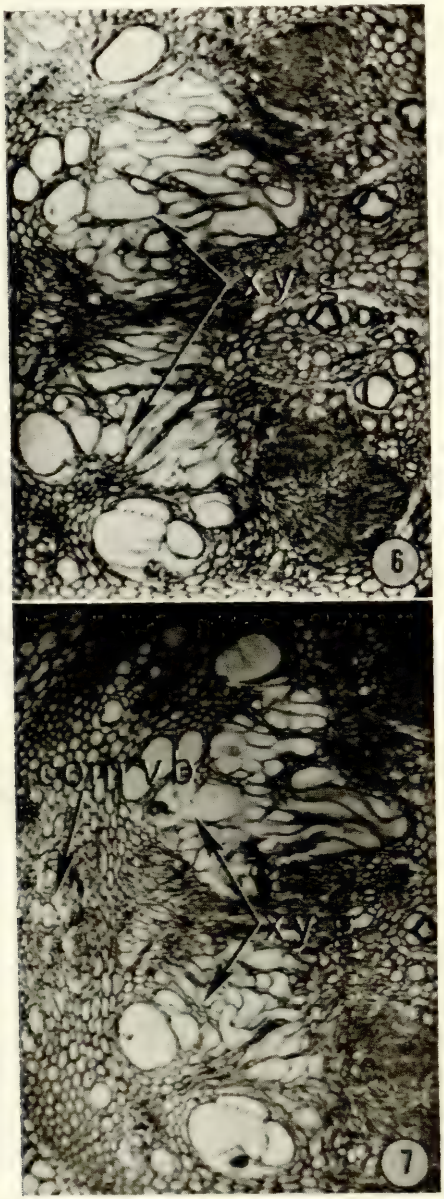


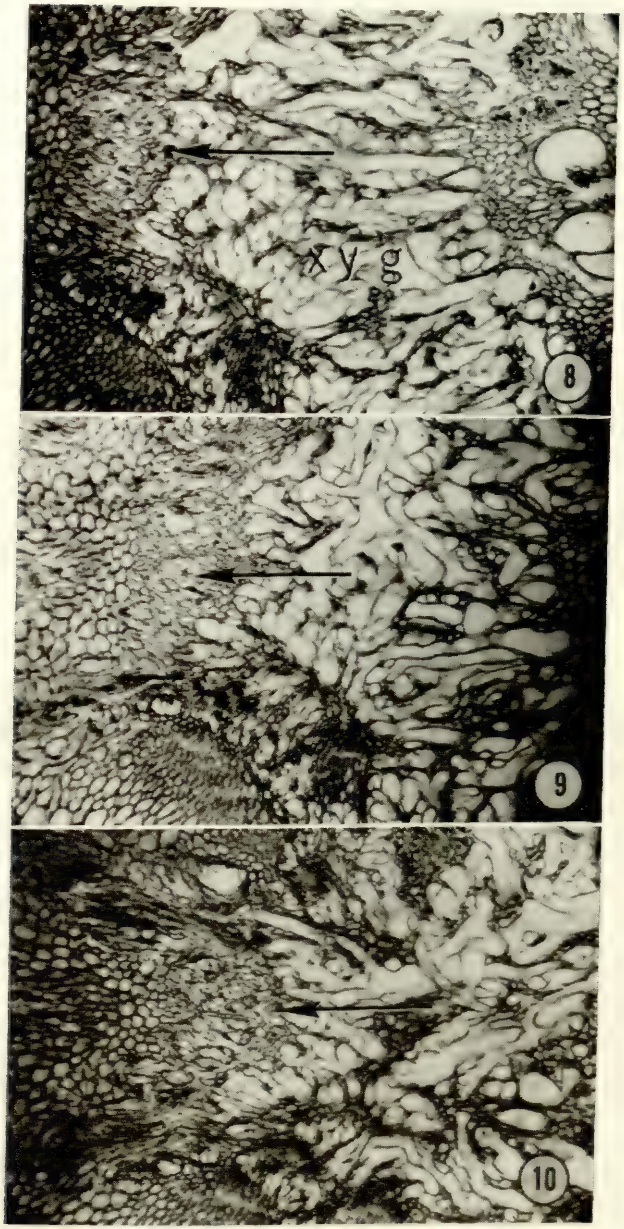
FIGURE 3. Internodal region where each vascular bundle maintains its individuality, × 105. Center arrow indicates direction of leaf insertion. Distance between FIGURES 3 and 4 is 380μ.

FIGURES 4 and 5. Large phloem units on inner side of the innermost pair of metaxylem vessels begin to break down and anastomose. × 105. Distance between FIGURES 4 and 5 is 150μ.



FIGURES 6 and 7. Large metaxylem vessels begin to lose their identity, × 105. Distance between FIGURES 6 and 7 is 80μ.

ABBREVIATIONS (for these and the figures which follow): ph. g., phloem glomerulus; xy. g., xylem glomerulus; com. v.b., common vascular bundle; cau. v.b., cauline vascular bundle; m. v., metaxylem vessel; ph. u., phloem unit; m. s., main stem; p., petiole; r. b., raphide bundles.



FIGURES 8–10. Sequence showing the "movement" of phloem and xylem glomeruli in the direction (arrow) of the point of the petiole insertion, × 105. Distance between FIGURES 8 and 9 is 20μ and between FIGURES 9 and 10 is 30μ.

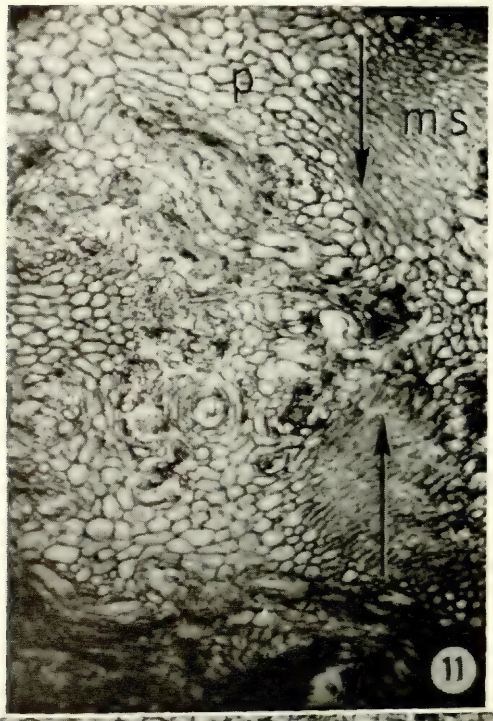
the reorganization is complete and internodal structure with usually 8 common and 8 cauline bundles is entirely restored.

DISCUSSION

Although the number of bundles varies between species, and the alternation of common and cauline bundles is an established fact, it has been observed that occasionally two common bundles "run" side by side. This irregularity may be explained as follows: At the node two cauline bundles originate in the plexus and take their positions in the spaces on either side of the middle common bundle and the lateral common bundles. This ratio of two cauline and three common bundles is corrected a little farther down the stem by the elimination in the plexus of one of the lateral common bundles. Therefore, in the internode there are almost always one or more common bundles in excess of the one to one ratio of common and cauline bundles. This irregularity is detected only in the internode because the common bundles never unite during their course in the internode. In a similar manner the cauline bundles of some specimens of *Dioscorea macroura*, *D. preussii*, and *D. sansibarensis* sometimes split into two with all the vascular elements above the pair of innermost metaxylem vessels forming a separate unit radially above the metaxylem.

Comparison of Dioscorea with Rhapis. In the course of this study it became quite obvious that the vascular architecture of *Dioscorea composita* was strikingly different from that of *Rhapis excelsa* (Palmae) described as a model for the monocotyledons by Zimmermann and Tomlinson (1965). Their detailed study of the vascular bundles revealed four types of branch systems. A leaf trace was found to originate by the gradual transformation of the vertical bundle which reaches its maximum size towards the center of the stem and turns sharply towards the stem periphery where it breaks up into several branches. The metaxylem deficient bundle that enters the leaf as a leaf trace was found to be the direct continuation of the vertical bundle. Zimmermann and Tomlinson (1965) concluded that there was no continuity of metaxylem between stem and leaf. Hence the leaf was irrigated solely by protoxylem. Apart from the studies on *Rhapis excelsa* the origin of the leaf trace and the discontinuity of the metaxylem into the leaf has also been demonstrated in other monocotyledonous genera including *Washingtonia*, *Geonoma* (Palmae), and *Prionium* (Juncaceae). The present study, however, has demonstrated that in *Dioscorea composita* (and in other species of Dioscoreaceae) the leaf is irrigated not solely by the protoxylem but by the metaxylem as well (FIGURES 6–8).

Zimmermann and Tomlinson (1965) also noted that in most cases a single vertical bundle arises from a trace plexus. However, they observed that in many cases two or more bundles may arise. The implication of this irregularity in the number of vertical bundles is that a certain measure of flexibility exists in the palms and in other monocotyledons which mani-



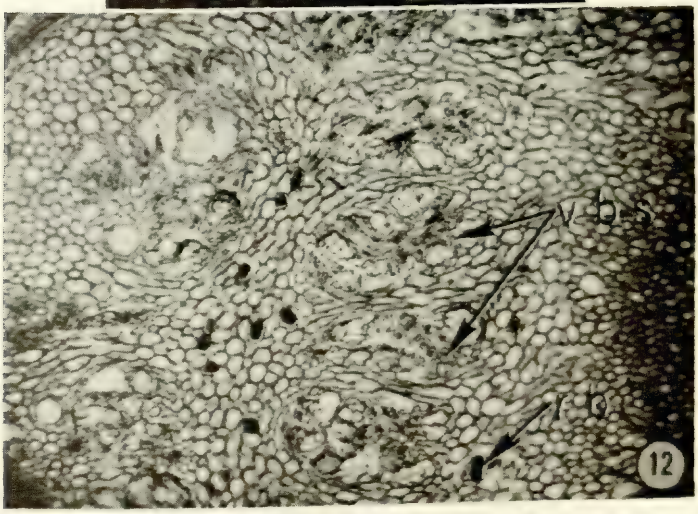


FIGURE 11. Arrows indicating the junction between the main stem and the petiole, × 105.

FIGURE 12. Transverse section of the petiole showing the reorganization of the vascular bundles in the petiole, × 105. Distance between FIGURES 11 and 12 is 40μ.

fests itself in the unequal, sometimes large number of bundles observed in stems.

The Dioscoreaceae exhibit remarkable constancy in the total number of bundles in the stem. With few exceptions, the number of cauline and common vascular bundles established early in ontogeny is maintained in the plant, regardless of the formation of xylem and phloem glomeruli that reduce all the vascular bundles entering the nodal region into a plexus.

The bridge bundles described and demonstrated in cinematographic analysis as branches from each departing leaf trace in *Rhapis* and *Prionium* were not encountered in *Dioscorea composita*. Bridges are short (the longest one measured in *Rhapis* is 4.5 mm.) and they make a leaf trace and a vertical bundle appear to fuse directly. If we were to assume that bridge bundles were indeed present in the Dioscoreaceae they must emerge from the leaf trace together with the vertical bundles in a single package.

Satellite bundles which Zimmermann and Tomlinson (1965) described as vascular branches from larger leaf traces originating in the region of bridge production were not observed in *Dioscorea composita*. Satellite bundles are best observed in plants which have fully developed inflorescences. Zimmermann and Tomlinson also stated that even in plants where inflorescences have aborted very early in their development and are not exomorphically visible, satellite bundles can still be detected.

These comparisons drawn between the Palmae and the Dioscoreaceae after using similar instrumentation and methods confirm the fact that the vascular systems of these two taxa are basically different. This study also contradicts the earlier belief (cf. Falkenberg, 1876; Mohl, 1845) that the Palmae and the Dioscoreaceae do share a common architectural framework.

The use of the Palmae as a model for the representation of the course of vascular bundles in the stems of monocotyledons is being questioned by some plant anatomists in view of the uniqueness of the palms amongst the monocotyledons. Vascular pattern studies in such genera as *Tradescantia* (Scott & Priestly, 1925), *Alstroemeria* (Priestly, Scott, & Gillett, 1935), *Ananas* (Krauss, 1948), *Oryza* (Majumdar & Saha, 1957), *Zea* (Kumazawa, 1961), *Ripogonum* (Simpson & Philipson, 1969) and my own unpublished data on the bamboo *Shibutaea kumusaca* and *Smilax megalantha* have shown conclusively that because of distinct variations which exist it is too early yet to consider the structure of any one taxon as a model for the Monocotyledoneae.

SUMMARY

The complex vasculature of the aërial stems of *Dioscorea composita* was traced through the use of the Optical Shuttle method and the Data Analyser Projector. This cinematographic analysis has shown that the course of vascular bundles in *D. composita* and the other species of Dioscoreaceae so far examined, differs markedly from that of the palm

Rhapis excelsa. Furthermore, the commonly held view that the Dioscoreaceae and the Palmae share a common vascular framework is not supported. In view of the variations that exist in the vascular patterns in a number of monocotyledons, it is suggested that the selection of any one taxon as a typical monocotyledon should await results of further studies.

ACKNOWLEDGMENTS

I wish to express my appreciation of the efforts of Miss Monica Brookman-Amissah who prepared the serial sections for this study. The study was supported in part by a grant from the Smithsonian Research Foundation.

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THE TAXONOMIC STATUS OF PROTOCYRTANDRA (GESNERIACEAE)

GEORGE W. GILLETT [1]

THE GENUS *Protocyrtandra* is based upon *Cyrtandra todaiensis* Kanehira, of which the type (*Kanehira 1854*) was collected on the island of Korror, Palau, Caroline Islands, and described in 1933. In 1934, Hosokawa gave generic rank to this taxon on the basis of "4 perfect stamens sitting freely with each other." The purpose of the present paper is to present an amplified description and an illustration of *C. todaiensis*, to relate its geographical location to the distribution of the genus, and to clarify its taxonomic status.

It must be emphasized that *Cyrtandra* is a little studied assemblage of some 600 species in which there is a remarkable propensity for evolutionary change, this being most noticeable in the morphology of the flower. The center of diversity for the genus is in the region of New Guinea, the Celebes, and Borneo, where there are about 300 species. In the territory from the Solomon Islands and Queensland, extending west and north to the Nicobar Islands and Botel Tobago Island (map, FIGURE 1) there are perhaps 400 species. The genus is distributed from this area north and east to islands of the Pacific on which there are an estimated 200 species, over one-half of which are endemic to the Hawaiian Islands. The extensive distribution of this genus and of a multitude of other insular Pacific genera defies explanation on other than speculative terms. Perhaps the most conservative speculation that can be advanced for *Cyrtandra* is that dispersal was accomplished by frugivorous birds adapted to the conspicuous, fleshy fruits and very small seeds (Guppy, 1906; Carlquist, 1967; Gillett, 1967).

Cyrtandra is adapted to almost continually wet, well-shaded habitats in forested ravines and gullies. Dispersal, therefore, has been limited almost exclusively to those "high" islands on which there is an abundance of rain forest vegetation. There are no cyrtandras on Yap, a "high" island on which the rain forest, presumably, was long ago removed by cultivation. No *Cyrtandra* has been collected on Niihau in the Hawaiian Islands. Although Niihau rises to approximately 400 meters, it is situated in the rain shadow of the island of Kauai and therefore has no rain forest vegetation. No *Cyrtandra* species occur in the Tuamotu Archipelago, an assemblage of "low" islands; none are known in the Marshall Islands, also "low" islands.

The genus *Cyrtandra* has a remarkable diversity in habit, occurring as herbs, shrubs, trees, or vines. The leaves are always simple, but may be

[1] Supported by the National Science Foundation and the Committee on Research, Academic Senate, University of California.

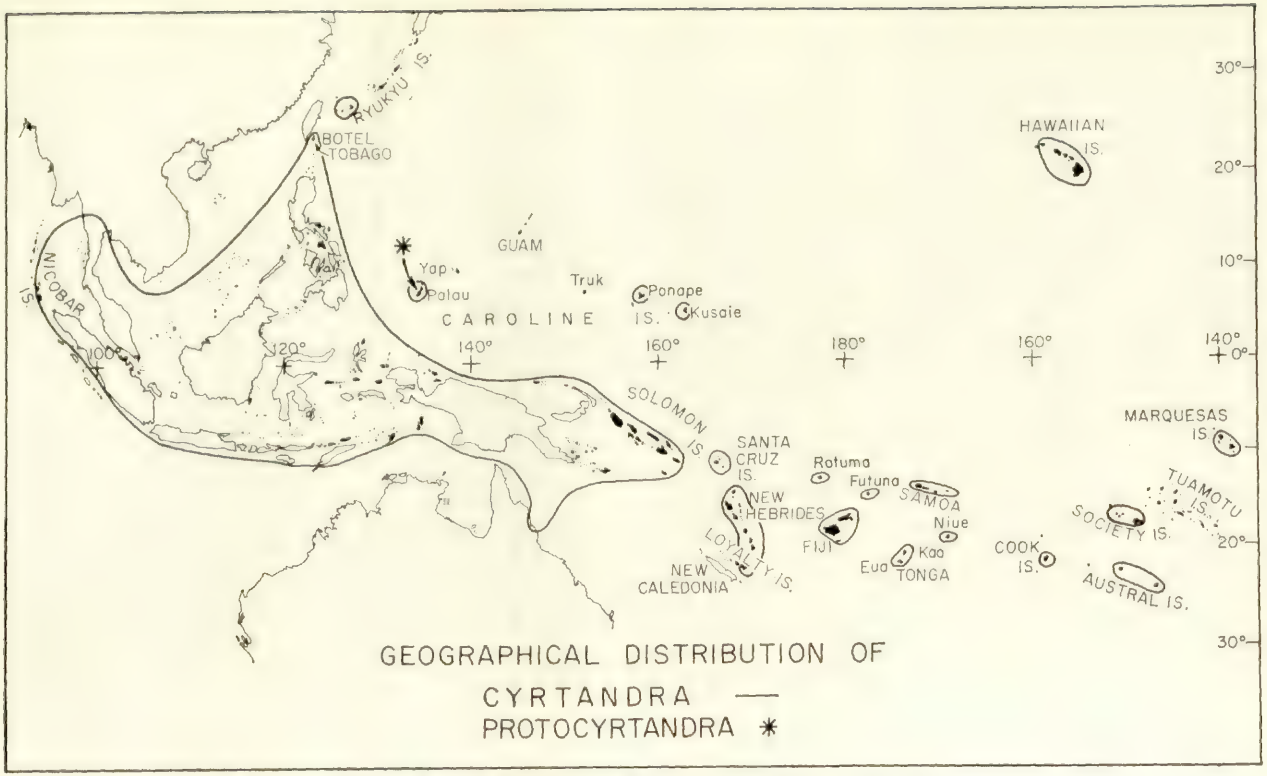

FIGURE 1. Map showing distribution of *Cyrtandra* and *Protocyrtandra*.

alternate, opposite, or whorled, with a diverse expression of marginal detail and indument. The flowers are extremely variable in form, most often with two stamens having coherent anthers and three staminodes, sometimes with the stamens not united, and occasionally (St. John, 1966) with sterile anthers borne on the staminodes. Therefore, the presence of four or five fertile stamens in the flowers of a given species does not seem particularly notable. While zygomorphy is the rule for the genus as we now know it, the corollas of some Hawaiian species come remarkably close to actinomorphy. It seems reasonable to predict that valvate, actinomorphic corollas, now known only in *Cyrtandra todaiensis*, will be found in other species.

It is appropriate to point out that several species of *Cyrtandra* are distinguished by possession of unisexual flowers. These species occur in New Guinea, the Solomon Islands, Fiji, and the Hawaiian Islands. The first to be discovered was accorded generic rank, as *Cyrtandropsis*, by Lauterbach (1910), and other species were added by Schlechter (1923). The genus was reduced by Burtt (1936) on the grounds that species with unisexual flowers thus brought together were very different in other characters. The propensity for the evolution of unisexual flowers is so widespread in Pacific genera (Carlquist, 1966) that their occurrence in *Cyrtandra* must be taken as an insignificant variation on a very common theme. If we were to give generic status to those populations of *Pittosporum*, *Wikstroemia*, *Santalum*, *Geniostoma*, *Alectryon*, *Pisonia*, *Styphelia*, *Myrsine*, and of other Pacific genera in which unisexual flowers have evolved, the proliferation of new genera would be ludicrous. It is my judgment that this same reasoning applies to evolutionary changes in the number of stamens in *Cyrtandra*.

Generic status for *Cyrtandra todaiensis* is rejected at this time because I believe there is a strong possibility that a definitive study of *Cyrtandra* will reveal intermediate expressions and character combinations that would make *Protocyrtandra* untenable. In this era of proliferation of new genera, it is held that a new genus must be demonstrated to be distinct *before*, not after, it is proposed. Such proof can be provided in this instance only by a review of all of the 600-odd species of *Cyrtandra*, after which an enduring decision can be reached as to whether this species should be accorded sectional, subgeneric, or generic rank.

It is a great pleasure to acknowledge the assistance of Mrs. Sheila A. Hardy, who collected in the Palau Islands during her recent tenure as a Peace Corps volunteer in the Caroline Islands. Mrs. Hardy was assisted by Mr. Demei O. Otobed, who unerringly guided her on several field trips. The field work of Mrs. Hardy and Mr. Otobed provided a mass collection, including spirit collections of flowers and fruits. The following description was prepared from the study of this extensive material. The illustration of *Cyrtandra todaiensis* was prepared by Mrs. Marion R. Sheehan. The manuscript was constructively reviewed by Mr. B. L. Burtt, Royal Botanic Garden, Edinburgh, to whom appreciation is extended.

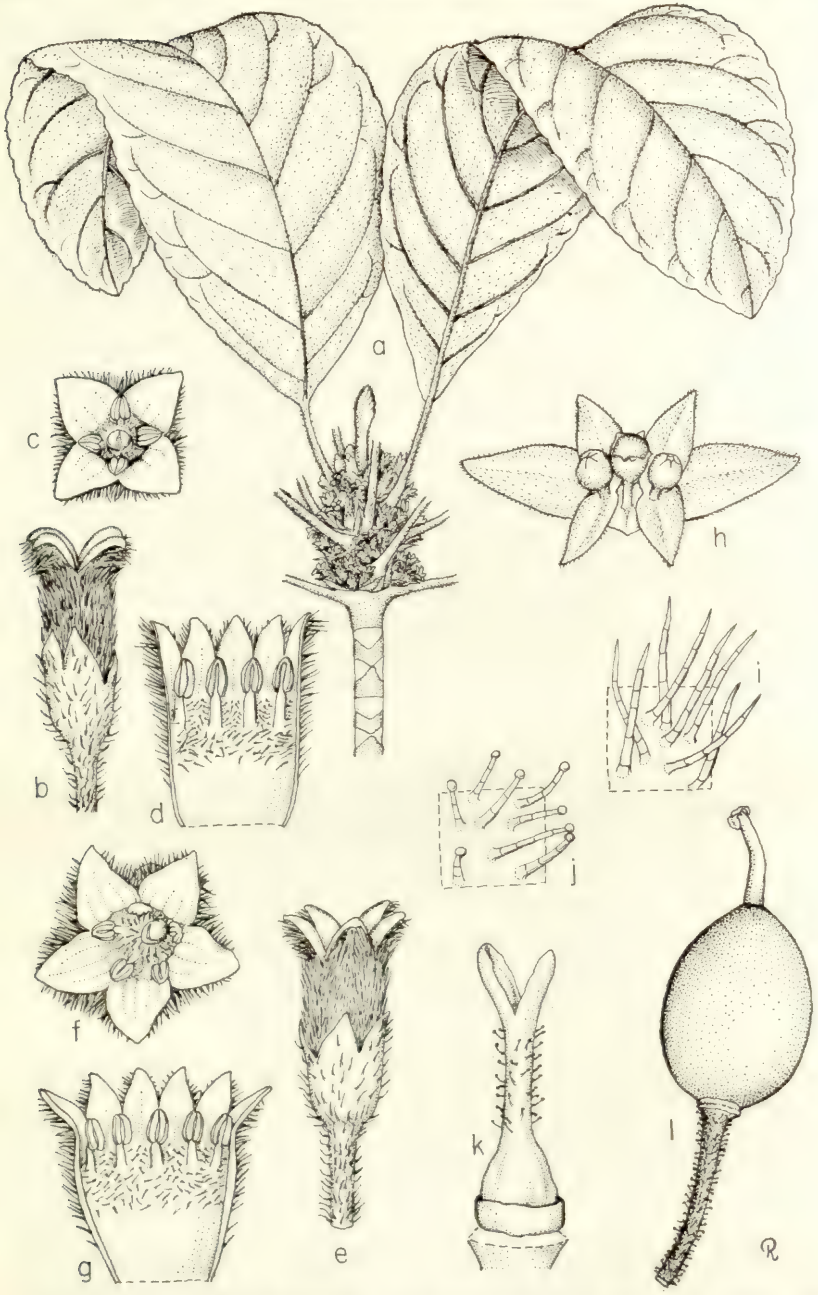

FIGURE 2. *Cyrtandra todaiensis*. All drawings from *Hardy & Otobed s.n.* a, flowering branch, × 1/4; b, 4-stamen flower, × 2; c, same in plane view,

Cyrtandra todaiensis Kanehira, Bot. Mag. Tokyo **47**: 679. 1933.

FIGURE 2.

Protocyrtandra todaiensis (Kanehira) Hosokawa, Trans. Nat. Hist. Soc. Formosa **24**(*132*): *202, 203.* 1934.

Erect shrub 2–3 m. high with pubescence of light brown, septate, uniseriate, noncapitate hairs ca. 30μ in diameter and 1 mm. long; mature stems up to 2 cm. in diameter, round in cross section, fistulose; young foliage densely lanate with light brown hairs; leaves decussate, glabrate at maturity, the petioles glabrate, up to 14 cm. long, connate at bases, the blades lanceolate to oblanceolate to elliptic, up to 40 cm. long and 20 cm. broad, unequal and acute to cuneate at base, acute to rounded at apex, undulate to entire at margins, the venation obscure above, conspicuous beneath, the primary veins 10–14 per side, curved apically and distally parallel to the margin, the secondary veins concealed above, reticulate below; inflorescence a congested, sessile, bracteate cyme of 15 to 20 pedicellate flowers, the outer bracts villose, lanceolate to oblanceolate, 2 cm. long and 0.5 cm. broad, the inner bracts of similar shape but smaller, deciduous; flowers perfect, borne on pedicels 0.5 to 1.5 cm. long, the calyx foliaceous, deciduous, up to 12 mm. long, cleft into 3, 4 or 5 unequal or equal, valvate lobes ca. 7 mm. long, densely pubescent on outer surface with noncapitate hairs ca. 60–120μ in diameter and up to 4 mm. long, glabrous on inner surface; corolla actinomorphic, up to 17 mm. long, cleft into 4, 5 or 6 equal valvate lobes ca. 5 mm. long, pilose on the outer surface with noncapitate hairs ca. 90μ in diameter and 2 mm. long, within pubescent at middle of tube with multicellular, uniseriate, non-capitate hairs (below) and capitate hairs (above) ca. 60μ in diameter and 1 mm. long; stamens 4, 5 or 6, the glabrous filaments 3 mm. long and adnate at the middle of the corolla tube opposite and slightly below the sinuses of the corolla lobes, all bearing fertile anthers ca. 3 mm. long, the anthers not coherent; cupulate annular disc conspicuous at base of ovary, ca. 1 mm. high; ovary and style ca. 8 mm. long, the ovary glabrous, the base of the style with capitate glandular hairs, the style cleft horizontally at the dilated apex into 2 applanate stigmatic lobes ca. 2 mm. long, the style separating ca. 1–2 mm. above the summit of the mature fruit; fruit a white, slightly translucent, ovoid, succulent berry with thick, fleshy pericarp and thin, intrusive placentae, up to 1.5 cm. broad and 2 cm. long, the apex rounded; seeds numerous, 2/3 mm. long, ovoid, foveolate.

SYNTYPE. Caroline Islands, Palau, Korror (Koror) Island, Todaiyama, 150 m. in dense, wet jungles, August 1932, *Kanehira 1854* (K).

× 2; d, same, showing interior of corolla, × 2; e, 5-stamen flower, × 2; f, same in plane view, × 2; g, same showing interior of corolla, × 2; h, young inflorescence, × 1; i, multicellular hairs of outer surface of corolla, × 20; j, multicellular colleters of inner surface of corolla, × 20; k, ovary from mature flower, × 4; l, mature fruit, × 2.

Caroline Islands. Toirechuil, Palau group. Growing in a limestone "sink" under dense canopy of shrubs and trees approximately 10 meters above the sea, *Hardy & Otobed, s.n.* (13 specimens) (A, BISH, E, UC, US).

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HAPLOID AND DIPLOID POLLEN IN HYPERICUM PATULUM

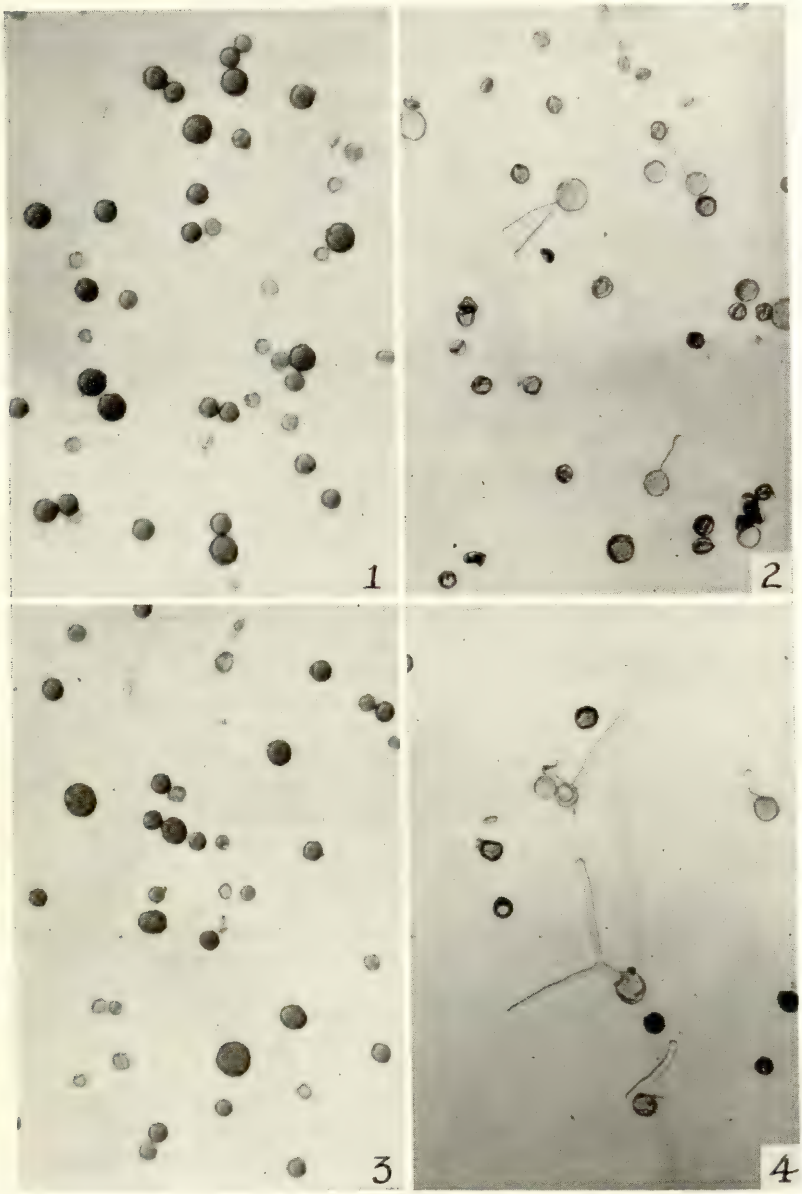
JOAB L. THOMAS *

HYPERICUM PATULUM Thunb. is a spreading shrub, native to Japan and China, but frequently cultivated elsewhere. It is evergreen or semi-evergreen in the southeastern states, but is killed to the ground each year in the Boston area. Even in areas in which it is winter-killed it grows to be 3 to 4 feet high each year, with a rounded growth habit. Cymes of golden yellow flowers 1½ to 2 inches across appear throughout July and August. *Hypericum patulum* var. *Henryi* Bean has larger flowers, 2 to 2½ inches across, and from this variety several cultivars have been derived, including 'Sungold', 'Hidcote', and 'Golden Cup'. The cultivars have even larger, usually darker colored flowers and are more profusely blooming.

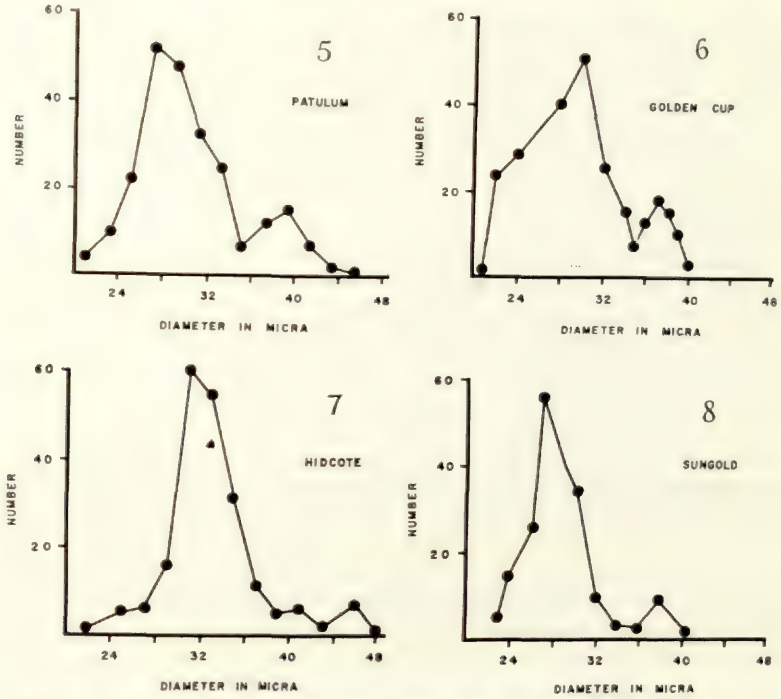
Polyploidy was suspected and a study of mature pollen from herbarium specimens revealed both a high percentage of abortive grains and an unusually large size variation in those appearing normal and staining normally with acetocarmine (FIGURES 1 and 3). Subsequent studies of pollen from buds of fresh material just prior to anthesis showed that the percentage of abortive grains, as determined by staining reaction with either acetocarmine or cotton blue, varied from a low of 30 percent in typical *H. patulum* to a high of 69 percent in the cultivar 'Golden Cup'. Size frequency plots for normally staining grains are shown in FIGURES 5 to 8. The size range is unusually high in this material, the diameters varying from 18 to 45 micra for grains taken from a single anther. In each case the size frequency curve is slightly bimodal, and although there were intermediates, there were two fairly obvious size categories. These are readily apparent in FIGURES 5 to 8. Although each of the graphs shown was made using measurements taken from a single flower, more than one anther was used in order to obtain a larger number of pollen grains. The pattern is essentially the same, however, when pollen from a single anther is measured. Samples from *Hypericum patulum* and *H. patulum* 'Hidcote' were examined using a single anther. Dividing the pollen grains into three groups, large, small, and abortive, the following counts were made; *H. patulum*: 165 large, 378 small, 547 abortive; *H. patulum* 'Hidcote': 111 large, 203 small, 679 abortive.

Germination tests, using a weak sugar solution, revealed that both size groups germinate, apparently with equal frequency (FIGURES 2 and 4). Moreover, pollen tube growth for the first three hours following germination seemed to proceed at approximately the same rate in the different size categories, although measurements of tube length were made on only a small number of cells.

* I wish to acknowledge the help of Dr. Otto Solbrig who read the manuscript and made useful suggestions.



FIGURES 1–4. Pollen grains from living material of *Hypericum patulum* collected approximately 24 hours before anthesis. FIG. 1, *Hypericum patulum* 'Hidcote'. FIG. 2, *Hypericum patulum*. FIG. 3, *Hypericum patulum*. FIG. 4, *Hypericum patulum* 'Sungold'. Photographed at an initial magnification of approximately 430 ×. Further explanation in text.



FIGURES 5–8. Size frequency plots for pollen grains which showed a normal staining reaction with acetocarmine. FIG. 5, *Hypericum patulum*. FIG. 6, *Hypericum patulum* 'Golden Cup'. FIG. 7, *Hypericum patulum* 'Hidcote'. FIG. 8. *Hypericum patulum* 'Sungold'.

A chromosome number of $2n = 36$ was reported by Sugiura (1936) for *Hypericum patulum*, from material cultivated in a botanical garden. No other counts for this species were reported by Robson and Adams (1968) in a recent survey of chromosome numbers in *Hypericum* and related genera. In the present study chromosome counts and pollen measurements were made on each of the varieties and cultivars listed in TABLE I. All counts were made from plants in the living collection of either the Arnold Arboretum, Harvard University (AA), or the University of Alabama Arboretum (UA). Column 4 in the table indicates the source from which the material was obtained by the respective Arboretum. Unfortunately, no material from native populations was available for study.

TABLE I

Hypericum patulum	$n = 18$	AA 149–49	Kohankie Nursery
H. patulum var. *Henryi*	$n = 18$	AA 160–45	Kew Gardens, England
H. patulum var. ?	$n = 18$	AA 747–49	Glasnevin, Ireland
H. patulum 'Golden Cup'	$n = 18$	UA 73–67	Neosho Nursery
H. patulum 'Hidcote'	$n = 18$	AA 263–51	Wayside Nursery
H. patulum 'Sungold'	$n = 18$	UA 41–67	Interstate Nursery

All counts and measurements were made from acetocarmine squashes of anthers. Meiosis in the pollen mother cells showed irregularities, however, and there was some variation in chromosome number from one cell to the next. Bridge formation was of frequent occurrence in most of the material examined. In addition, the small and very sticky chromosomes in this species make this rather difficult cytological material. Pairing was irregular and multivalent formation was common. Both trivalents and quadrivalents were seen, with up to four multivalents occurring in a single nucleus. Univalents, too, were observed rather frequently. The univalents lag noticeably at anaphase and usually lead to the formation of micronuclei. This apparently accounts for the large number of abortive grains. Certain other pollen mother cells fail to undergo the second division of meiosis and form dyads rather than tetrads. These cells, therefore, retain the diploid chromosome complement which probably accounts for the very large grains. Preliminary observations indicate that dyad formation and giant pollen grains occur with about equal frequency in a given individual, although the number of dyads counted represented a rather small sample.

The remaining pollen apparently develops from tetrads following a more normal meiotic division. These occur with the greatest frequency, and with the various meiotic disturbances observed it is not surprising that there should be considerable variation in the size of the grains in this category also.

Additional work is needed on these interesting plants, particularly studies of megasporogenesis, and controlled pollination experiments. It should be particularly interesting to make cytological studies of this material from native populations. Although $2n$ pollen seldom competes successfully with $1n$ pollen (Burnham 1962) it is apparent that functional $2n$ pollen is produced by these plants in significant quantities.

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STUDIES IN THE LEGUMINOSAE, 11. A NEW SPECIES OF DERRIS FROM THE SOLOMON ISLANDS

K. THOTHATHRI

DURING A STAY at the Herbarium of the Komorov Botanical Institute, Academy of Sciences of the USSR, Leningrad, I came across an interesting specimen of *Derris* from the Solomon Islands (*Kajewski 2290*) which did not agree with material of any other species of this genus. After critical study, this specimen was found to represent a quite distinct undescribed species. Information was then requested from the Arnold Arboretum of Harvard University regarding the duplicates of the Kajewski collection. It was learned that these had been incorrectly identified as *Derris elegans* Benth. The characters of Kajewski's plant are so well marked that it is being proposed here as a new species.

Derris salomonensis Thoth., spec. nov. PLATES I, II.

Pertinet ad sect. DERRIS (§ *Euderris* Benth.) affinisque est *D. multiflorae* Benth., a qua tamen differt foliolis maioribus, inflorescentia glabra semper foliis breviore, pedicellis longioribus et ovario puberulo.

Planta volubilis in silva pluviali; ramuli glabri, lenticellati, striati. Folia imparipinnata, alterna, 32–40 cm. longa; foliola 5, ovato-oblonga vel oblonga, 14–22 × 6.5–9.5 cm., integra vel undulata ad margines, ad basin angustata, obtusa vel acuta, interdum breviter acuminata, subcoriacea, glabra, petiolulata, stipulata; nervi laterales 7–9-jugi, reticulati pulchre, rachide glabra; petiolulis 6–9 mm. longis; stipulis deciduis et stipellis linearibus. Inflorescentia axillaris racemosa, 9–12 cm. longa, multo foliis breviore rachide glabra. Flores 2–3 brevibus stipitibus insidentes e nodis emergentibus, 1–1.2 cm. longi; pedicelli tenues, 8–10 mm. longi, glabri vel minute puberuli; bracteae lineares, ad basin pedicelli; bracteolae binae, lineares, quarum una pedicello sub calyce ipso et alterna basi calycis insident. Calyx campanulatus, 1.5–2 × 2–4 mm., brunneus puberulus extus, integer vel molliter dentatus. Corolla alba, vexillum ovato-orbiculare, breviter unguiculatum, glabrum, 1–1.3 cm. longum, retusum vel emarginatum ad apicem; alae anguste oblongae, distincte unguiculatae, 0.9–1 cm. longae, auriculatae infra; carina navicularis, connata infra, 0.9–1 cm. longa, distincte unguiculata; stamina 10, monadelpha, columna 0.9–1.1 cm. longa, divisa supra; filamentis liberis in triente superiore, antheris versatilibus. Pistillum 1–1.1 cm. longum, ovarium non stipitatum, elongatum, puberulum, stylo curvato, stigmate obliquo, ovulis 3–4. Legumen ignotum.

TYPE. Solomon Islands. Bougainville Island, Karngu, 50 m., 22. 10. 1930, *S. F. Kajewski 2290* (LE, holotype; A, isotype).

The new species *Derris salomonensis*, a large climber in the rain forest, has handsome white flowers in pendent racemes. It is a member of sect. DERRIS (§ *Euderris* Benth.) and is related to *D. multiflora* Benth., from which it differs in its larger leaflets, glabrous inflorescence always shorter than the leaves, its longer pedicels and puberulous ovary.

The stamens of *Derris salomonensis* are basically monadelphous, but the vexillary filament is always free at the base and in its upper portion; it is united with the column only in the middle portion. The staminal column is split open dorsally and the other filaments are free for their upper third.

Additional material of this interesting new species, particularly in fruiting condition, would be most desirable.

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I wish to express my gratitude to Dr. J. T. Vassilczenko, Curator of the Herbarium, Komorov Botanical Institute, Leningrad, for according me facilities to pursue this work; to Dr. Father H. Santapau, Director, Biology Department, St. Xavier's College, Bombay, for the Latin translation of the description of the new taxon; to Dr. K. Subramanyam, Director, Botanical Survey of India, Calcutta, for his kind encouragement; and to Dr. Lorin I. Nevling, Jr., of the Arnold Arboretum and Gray Herbarium of Harvard University, Cambridge, Massachusetts, for kindly supplying information about the duplicates of the collection studied.

CENTRAL NATIONAL HERBARIUM
BOTANICAL SURVEY OF INDIA
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EXPLANATION OF PLATES

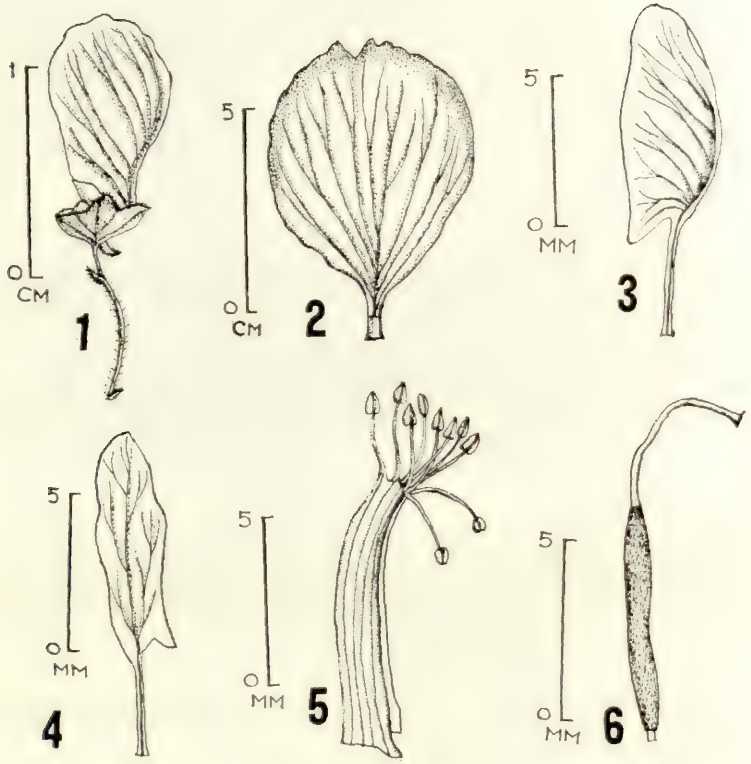
PLATE I

Derris salomonensis Thoth. Photograph of holotype, *Kajewski 2290* (LE).

PLATE II

Derris salomonensis Thoth. Drawings of flower parts. FIGURE 1. Flower, including pedicel and bracteoles; FIGURE 2. Standard; FIGURE 3. Wing; FIGURE 4. Keel petal; FIGURE 5. Staminal column; FIGURE 6. Ovary with style and stigma. Enlargements as indicated on each figure.

Thothathri, Derris



THOTHATHRI, DERRIS

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COVER: The Golden Larch, *Pseudolarix* Gordon

With volume 51 the *Journal of the Arnold Arboretum* begins its second half century of continuous publication. To celebrate the occasion we are pleased to present a new cover format. The cover design is the work of Norman Comeau of the Art Department, Thomas Todd Company, Printers, Boston. We hope from time to time to have drawings of other plants on the cover. The Table of Contents will appear on the back cover. *Eds.*

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THE GENERA OF ACANTHACEAE IN THE SOUTHEASTERN UNITED STATES [1]

ROBERT W. LONG

ACANTHACEAE A. L. de Jussieu, Gen. Pl. 102. 1789, "Acanthi," nom. cons.

(ACANTHUS FAMILY)

Herbs [shrubs] or vines [rarely small trees]. Leaves simple, opposite exstipulate; pubescence of stems and leaves of simple hairs; cystoliths of various forms often present in parenchyma or epidermis. Inflorescences basically cymose (dichasial), often condensed in leaf-axils, modified into racemes or panicles, or flowers sometimes solitary. Flowers perfect, nearly actinomorphic to zygomorphic; bracts and bracteoles usually present and often colored, sometimes large and enclosing the flower. Calyx segments 5, occasionally 4, not infrequently fused, persistent. Corolla sympetalous, the limb 5-lobed or bilabiate, rarely 1-lipped, lobes convolute or imbricate in bud. Nectariferous disk nearly always present, below ovary.

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). The treatment in this paper, which is the 52nd published in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which have not been seen and verified are marked by an asterisk.

The manuscript for this paper was prepared while I held a Mercer Research Fellowship at the Arnold Arboretum in the latter half of 1968. I want to express my thanks for the facilities extended to me during my stay in Cambridge and to the several people who have aided substantially with this treatment of the Acanthaceae. Dr. Carroll Wood has spent a great deal of time in editing and checking the manuscript, in making numerous additions and suggestions, in preparing the dissections for and supervising the illustrations, and in preparing the legends for them. The illustrations are the work of the late Dorothy H. Marsh (FIGURE 5, i–n) and of Diane C. Johnson and Virginia Savage, whose initials will be found on the appropriate ones. Mrs. Mary C. Dillon carefully checked most of the references and the abbreviations of books and journals, and Mrs. Nancy Dunkly verified most of the remainder and prepared the typescript. My appreciation is extended to them all.

Stamens 4 (5), didynamous, or 2 (staminodia often present in 2-stamened flowers, 1, 2, or seldom 3), epipetalous; anthers 1- or 2-loculate, longitudinally dehiscent, the connective of various widths; pollen very variable, of many kinds, mostly tricolporate. Gynoecium of 2 united carpels; stigmas simple or 2-cleft or -lobed, the posterior lobe often aborted or wanting; style filiform, simple; ovary 2-loculate, superior, placentation axile (parietal in Nelsonioideae), ovules 2–10 in each locule, anatropous, amphitropous, or campylotropous, 1-integumented, tenuinucellate. Fruit typically a 2-valved loculicidal capsule [drupaceous in Mendoncioideae]. Seeds 4(2)–20, usually flat, without endosperm [endosperm present in Nelsonioideae] borne on hooklike projections, the modified funiculi of the ovules, termed retinacula or jaculators, these papilliform or apparently lacking in a few genera; seeds usually dispersed through sudden opening of fruit; seed coat smooth or roughened, often mucilaginous when moistened; embryo straight or bent; cotyledons broad and flat. Embryo-sac development normal, monosporic (Polygonum type), embryogeny generally conforming to Onagrad type (Nelsonioideae) or Solanad type (Ruellioideae). Chromosome numbers $x = 7$–18, 20, 21. (Including Thunbergiaceae Bremek., Mendonciaceae Bremek.) TYPE GENUS: *Acanthus* L.

A pantropical family of about 250 genera and 2600 species with four main centers of distribution: Indo-Malaya, Africa, Brazil, and Central America. About 12 genera, including the two largest, *Justicia* (about 300 species) and *Ruellia* (about 225 species), are pantropical. Of the remaining genera about 40 per cent are confined to the Western Hemisphere. Approximately 120 genera are monotypic and restricted in range. Relatively few taxa are found in the United States; only three genera occur in the Northeastern States, seven additional ones are indigenous to the Southeastern States, and a few more are represented by species in the southwestern United States.

The family has long been noted for its taxonomic difficulty. Some authorities (e.g., Lindau, Grant, Melchior) consider the Acanthaceae to be a natural family, presumably monophyletic in origin, while others (e.g., Van Tieghem, Bremekamp) have viewed the original composition of the group as being artificial, presumably polyphyletic. For the great majority of genera the family may be recognized by the presence of the peculiar structure of the funiculus that becomes hook-shaped in the mature fruit, and is termed the retinaculum or jaculator. This structure, however, is not typical of three of the subfamilies that contain a few genera of uncertain relationship.

The family also is characterized by the presence of cystoliths in the leaves and stems of most (but not all) genera and by the explosive dehiscence of the mature capsule. Cystoliths are visible as slight protuberances or, more commonly, as streaks in the epidermis. Bracts and bracteoles are generally present and are often showy. Classification within the family is based primarily on minor characters of the androecium, particularly the anthers, and on pollen sculpture. Such bases for classification

often make difficult the accurate identification of genera and species. A wide variety of life forms is found, including many hygrophiles, xeromorphic species with spiny or acicular leaves, lianas, and even mangrove plants. Arborescent forms are rare, and most species are shrubs or herbs with opposite, usually decussate, entire, exstipulate leaves. In the tropics the Acanthaceae, particularly the "Strobilanthes" group of the Old World, are conspicuous, showy elements of the local vegetation. Santapau, for example, listed 42 genera found in the immediate vicinity of Bombay, India.

Various genera have been the subject of anatomical and morphological investigations. Detailed accounts and references have been given by Solereder, who also made special reference to the occurrence and morphology of cystoliths. These appear in the form of silicified bodies with or without a cellulose skeleton. Linsbauer earlier had shown that their nature and distribution are valuable in the recognition of genera, especially in the Ruellieae and Odontonemateae. Slightly lignified cystoliths occur in the pith of certain species of *Ruellia*, and pigmented cystoliths are reported for *Ruellia*, *Sanchezia*, and *Strobilanthes*. In addition to cystoliths, calcium oxalate crystals may be secreted in the form of prisms, needles, or other shapes.

Solereder reported that petiolar anatomy exhibited either a single arc-shaped vascular strand, or a concentric group of separate bundles with the ends of the crescent very much incurved in some species, or a circle of more or less separate bundles (e.g., *Thunbergia*), or, rarely, a cylindrical vascular strand (e.g., *Crossandra*). The epidermis is occasionally papillose (e.g., *Ruellia*). Stomata are present on both leaf surfaces in some species but are confined to the lower surface in others, and they are nearly always caryophyllaceous, although in at least *Lepidagathis* they are rubiaceous. A wide assortment of both glandular and nonglandular hairs is reported for various genera.

The family is characterized anatomically by the presence of anomalous secondary thickening that occurs in a number of genera. This usually appears as inconspicuous groups of intraxylary and interxylary phloem and as bundles of bodies (described as acicular fibers) that resemble large raphides. The vessels typically are very small (less than 50μ) or extremely small (less than 25μ). Wood is semi-ring-porous, and the vessel elements have fine, spiral thickenings, simple perforations, and scanty parenchyma. The vascular system of *Justicia americana* has been found to consist of seven distinct steles, one central and six arranged around the circumference. The meristeles and the central medullary bundle anastomose at the node. The axis of the inflorescence in most genera is monostelic, but in some respects the stem anatomy resembles certain Campanulaceae because of the presence of a medullary bundle. The roots generally contain less well-developed xylem. Unusually long root hairs, intraxylary phloem, and pitted lignified pith are also recorded for certain genera.

The anatomy of several Ruellieae, including *Blechum*, *Dyschoriste*,

Hemigraphis, *Hygrophila*, and *Ruellia*, has been described in detail by Tchouproff, who also attempted, rather unsuccessfully, to show relationships graphically by means of anatomical comparisons. Danert analyzed leaf, bud, and floral arrangements in selected genera, including *Blechum*, *Justicia*, *Ruellia*, and *Thunbergia*. He concluded that Acanthaceae exhibit "plagiotropic" growth owing to the presence of a "Sprossendodermis," a character he attributed to phylogenetically older stocks. Vesque suggested an anatomical characterization of the family, but only in connection with the leaf anatomy. He also gave a classification of cystoliths.

The Acanthaceae have long been notorious for their very great variation in pollen morphology, useful in taxonomic diagnosis. Probably no other family has such a wide range of pollen morphological features as the Acanthaceae. Early detailed studies of acanthaceous pollen were made by Bischoff, Fritzsche, and Von Mohl, but the taxonomic value of pollen characters in the classification of the family was first pointed out by Radlkofer. It was on the basis of his work that Lindau elaborated the use of pollen morphology as the chief basis for his classification of the family in Engler & Prantl's *Die Natürlichen Pflanzenfamilien*. Hallier, who reported both three-porous and sparsiporous grains in *Pseuderanthemum*, was among the first to question seriously whether pollen is any more valid than floral morphology as a tool for determining relationships. Later students of the family have continued to emphasize the use of pollen, however.

Raj, after an exhaustive survey of pollen types in 260 species of 103 genera, concluded there are considerable grounds for doubting the convincing use of pollen as a basis for classification, although he apparently is in general agreement with Bremekamp's use of pollen in his revisionary studies. The Thunbergioideae have the largest pollen, varying from 60 to 100 μ, anomatreme, spheroidal, eight-colpate; Nelsonioideae show much less variation and typically have three-colpate, prolate pollen; the Acanthoideae sensu Lindau have a very wide range of pollen types, including two-porate bilateral, pantoporate, polyporate, and the most common form, three-colporate, found in most of the tribes. Although many tribes form homogeneous groups, others, such as the Ruellieae and Odontonemateae, have various kinds of pollen sculpturing.

Recent studies of pollen and its use as a taxonomic tool in the family have not been altogether reassuring. Bhaduri concluded that the pollen of Nelsonioideae closely resembles that of *Andrographis* (Ruellioideae), although Raj strongly disagreed. Sharma & Vishnumittre found four widely different pollen types in *Eranthemum* and *Pseuderanthemum*. Bremekamp's rearrangement of tribes and genera is based primarily on his interpretation of pollen relationships. This has led him to recognize a number of segregate genera, especially in the Ruelliinae, based on minor pollen differences. It has yet to be established whether or not these "splinter" taxa are worthy of recognition.

The Acanthaceae also have a great range of chromosome numbers. Twenty different haploid numbers have been determined, with $n = 7, 9,$

10, 13–22, 25, 26, 28, 30, 31, 34, 40, and 66. Basic numbers of (5) 6, 7, 8, 9, 10, and 11 are known, most species generally falling into one of three series, $x = 7$, 8, or 9, with $x = 7$ represented by the greatest number of genera. The lowest haploid number ($n = 7$) is found in *Thunbergia*; the chromosomes of *Elytraria* are among the smallest in the family, about 1μ in length chiefly with median centromeres. Pizzolongo & D'Arienzo examined *Acanthus* cytologically and reported the genus as dibasic, with $x = 7$ or 8; *A. spinosus* is a sterile polyploid with $2n = 112$, but the closely related octoploid *A. mollis*, $2n = 56$, and decaploid *A. montanus*, $2n = 80$, are fertile. Grant, who studied the family cytologically, largely to investigate generic relationships, concluded that polyploidy, especially aneuploidy, has undoubtedly occurred and that the wide range of numbers represents an ascending and descending aneuploid series. Aneuploidy is probably responsible for the large number of genera and species. Grant found that all but three of the 18 genera, where more than one species was examined, had euploids, aneuploids, or both types of polyploids present. Narayanan used cytological studies to demonstrate the close relationships of some genera and intrageneric groups. Grant also based some of his speculations regarding relationships within the Justicieae on chromosome numbers.

The considerable embryological literature in Acanthaceae has been reviewed by Schnarf, Mauritzon, and, most recently, by Maheshwari & Negi. Detailed references are also given by Davis. The linear tetrad develops into a Polygonum-type embryo sac; the embryogeny follows either the Onagrad (*Elytraria*) or Solanad type. Mauritzon pointed out that the endosperm shows a mode of development peculiar to the Tubiflorae; this is a cellular type of endosperm that results from free nuclear divisions followed by wall formation in the central chamber. The first two divisions result in a row of three cells which form the endosperm proper, while the micropylar and chalazal cells develop into haustorial organs. The chalazal haustorium is lacking in *Thunbergia*. Bhaduri concluded that *Acanthus* and *Crossandra* ought to be considered the basic type for the family because they lack the free nuclear stage. The advanced type would then be represented by *Ruellia* and *Adhatoda* (*Justicia*) where free nuclear divisions occur. Supernumeraries and persistent antipodals are found rarely in the family, although Hartman reported them in *Aphelandra*.

Embryological data have been adduced by Johri & Singh as evidence that the Nelsonioideae properly belong in the Acanthaceae, and not in the Scrophulariaceae, as proposed by Bremekamp, who discounted the importance of comparative embryological similarities in Acanthaceae. The family continues to provide considerable interest for the plant embryologist, however. A recent investigation by Sahi presented the details of the distinctive embryo sac and embryogeny of *Andrographis* that throw some light on the taxonomic relationships of this genus.

Unfortunately, the floral biology of the family is not as well understood as the embryology. Characteristically, the flowers are proterogynous, nectar-yielding, and brightly colored and are often arranged in large in-

florescences. Usually, insects hit the downward directed tips of the pollen sacs and are dusted with pollen on the back. The insect transfers the pollen to projecting stigmas of another flower. Premature dispersal of pollen is apparently prevented by the hairs that frequently surround the anthers. Highly specialized pollinating systems involving extrafloral nectaries have been reported in *Thunbergia*. Ornithophily (hummingbirds) and possibly myrmecophily may be factors in the pollinating systems of red-flowered rain-forest species of *Aphelandra*.

Uphof reported cleistogamy in six genera of Acanthaceae. Tharp & Barkley found that all paniculate taxa of *Ruellia* in Texas are cleistogamous, and Long & Uttal discovered that all species of *Ruellia* of the eastern United States are cleistogamous during part of the reproductive cycle. The general occurrence and importance of cleistogamy in Acanthaceae have yet to be evaluated, but they deserve further attention. Monocarpy apparently is common in the Old World genus *Strobilanthes*; after a number of years of vegetative growth, the plants flower, then die off. Santapau has observed, however, that renewed vegetative growth may occur after flowering in *S. callosus* Nees if there has been an abundance of rain.

Seeds are dispersed for short distances by the explosive dehiscence of the ripe capsule. Bremekamp attributed this mechanism to the progressive loss of water from the maturing fruit. Many genera have seeds covered with hairs or scales that become erect with moistening; possibly this is an adaptation that helps to anchor the seed in a suitable substratum.

Breeding studies and hybridization experiments are few in number. Meeuse & DeWet have reported natural and artificial intergeneric hybrids between the South African *Ruttya*, $2n = 36$, and *Ruspolia*, $2n = 42$. They suggested that the vigorous but completely sterile hybrid ($2n = 39$) may have horticultural value and that other intergeneric hybrids may occur. Lindau did not place these two genera in the same tribe. Long has made numerous intrasectional and a few intersectional hybrids in *Ruellia*. Investigations reported thus far suggest that large scale cross-breeding work in Acanthaceae would be of considerable value both taxonomically and horticulturally. Perhaps the difficulty of obtaining materials of this largely tropical group accounts for the dearth of genetic experiments in the family.

Little is known about the phytochemistry of the family, perhaps because no important poisonous, medicinal, or useful species are known. Pharmacological investigations of drugs from certain genera have been made, and diuretic and antiasthmatic effects have been credited to members of the family. Chemical constituents include polyphenols, essential oils, non-volatile isoprenoid compounds, heterosides, and alkaloids. Arndt, Eggers, & Jordaan have determined by spectrographic analysis the structure of five new alkaloids obtained from the South African genus *Anisotes* and some flavenoid studies have recently been reported by Nair. Obviously, much remains to be learned concerning the chemotaxonomy of genera in the family.

The Acanthaceae have had a long, tortuous history, taxonomically, since they were first recognized as "Acanthi" by B. de Jussieu in 1759. The

name was adopted by A. L. de Jussieu, who placed eight genera in the group. A general discussion of the family and its affinities was given by Lindley, who included a list of genera supplied by Nees and references to the early literature. Nees's account in De Candolle's *Prodromus* was the first comprehensive treatment of the family, and it established limits for many genera that have been followed up to the present. Endlicher, following Nees, divided the "order" Acanthaceae into three tribes, Thunbergieae, Nelsonieae, and Echmatacanthi, the last further divided into seven subtribes. On the basis of floral morphology Bentham & Hooker recognized 120 genera in five tribes: Thunbergieae, Nelsonieae, Ruellieae, Acantheae, and Justicieae, with the Ruellieae further divided into five subtribes, the Justicieae into six.

Radlkofer demonstrated the value of pollen characters in the classification of Acanthaceae and, as mentioned above, Lindau greatly expanded the critical use of pollen characters in his treatment of the family. Lindau distinguished four subfamilies, Nelsonioideae, Mendoncioideae, Thunbergioideae and Acanthoideae. Van Tieghem proposed that the "Thunbergiacées" be a separate family to consist of three tribes, "Thunbergiées," "Mendonciées," and "Nelsoniées." He proposed dividing the remaining Acanthaceae into two subfamilies, the "Acanthoïdées" (without cystoliths), and the "Justicioïdées" (with cystoliths). Wettstein was in general agreement with this change because he concluded there was close affinity between Lindau's first three subfamilies. However, instead of regarding them as a distinct family, he placed them all in Thunbergioideae, thereby reducing Lindau's subfamilies to tribes. Interestingly, this was the original position taken by Nees, whose Anechmatacantheae (without retinacula) and Echmatacantheae (with retinacula) correspond to Wettstein's Thunbergioideae and Acanthoideae.

More recently, Bremekamp has made a revision of the family based largely, but not entirely, on detailed pollen characters. He divided the Acanthoideae sensu Nees into Acanthoideae and Ruellioideae, while abandoning Lindau's familiar "Contortae" and "Imbricatae." Lindau's 16 tribes were reduced to seven, largely through transfers and expansion of tribal circumscriptions. Bremekamp changed his mind about an earlier reduction of Nelsonioideae to a mere subtribe of Acantheae and removed them from the family, recommending they be placed in the vicinity of the Rhinantheae (Scrophulariaceae). He raised Lindau's Mendoncioideae and Thunbergioideae to family status and made numerous changes in generic limits, especially in Old World tropical taxa. On the basis of his palynological studies, Raj concurred with Bremekamp's revisions, but Grant said there is no "cytological criterion" to suggest that the subfamilies are sufficiently different to be considered separate families. Grant maintained that the evidence from chromosome studies suggested that a classification based on pollen morphology may be somewhat artificial.

Wernham suggested that the Thunbergieae are closely related to the Convolvulaceae, but that they ought to be classified with Acanthaceae because of their "primitive" retinacula. Melchior maintained the same

general classification of the family as Lindau, while admitting that the subfamilies are indeed strongly marked. Leonard also followed Lindau's circumscriptions in his treatment of tropical American groups.

Changes in and additions to the general classification of Acanthaceae continue to the present, with the general tendency of one school (represented by Bremekamp and Raj) to emphasize minor differences in pollen morphology, anther, and other floral characters in recognizing numerous segregate taxa; and the other school (represented by Melchior and Leonard) to follow the broad generic interpretations of Lindau. Melchior stated the situation accurately when he said, "Auch die natürliche Gliederung der Acanthaceae . . . ist noch in Fluss."

The phylogenetic relationships of Acanthaceae are also controversial. Baillon thought the family was related to both the Scrophulariaceae and the Labiatae on the basis of stamen morphology and to the Bignoniaceae on the basis of calyx and fruit characters. He thought Acanthaceae were also related to Boraginaceae and to Convolvulaceae through their nearly actinomorphic flowers. Bessey considered Acanthaceae as descended from Scrophulariaceae or groups ancestral to them. Engler and Diels placed the family between Globulariaceae and Myoporaceae in the vicinity of the large and complex Gesneriaceae. Hegnauer, on the basis of phytochemical evidence, suggested that there is close relationship with the Verbenaceae-Labiatae complex, but he may also have been influenced by Wettstein, who had placed Acanthaceae in the Tubiflorae between Bignoniaceae and Verbenaceae. Apparently, students generally agree that Thunbergioideae is the most primitive subfamily on the basis of anatomical, embryological, cytological, and palynological grounds.

Melchior considered the family to be an old, highly developed and very natural group distinguished by the "sling mechanism," pollen morphology, and the presence of cystoliths and thought that certain parallel developments have occurred in the closely related Scrophulariaceae. Bremekamp stated a diametrically opposing view that Acanthaceae sensu Lindau cannot be regarded as a natural entity. He attempted to resolve this problem by excluding what he considers are extraneous elements, as the Thunbergiaceae, the Mendonciaceae, and the Nelsonieae. Bremekamp's "natural" Acanthaceae is closely similar, then, to Lindau's subfamily Acanthoideae. Raj concluded from his pollen studies, particularly of the sporoderm, that Acanthaceae sensu Bremekamp is an assemblage of primitive and advanced tribes. He concluded that the Strobilantheae, Barlerieae, and Andrographideae are primitive, while Justicieae, Aphelandreae, and Acantheae are the most advanced.

As in most angiospermous groups, there is a sketchy fossil record. Velenovsky & Viniklar believe Acanthaceae date back to Cretaceous times because of their identification of fossils as *Strobilanthes*. Raj, from photographs by Kuyl, Muller, & Waterbolk, identified fossil pollen taken from Miocene deposits as resembling that of *Ruellia* and *Sanchezia*. Because there are so few tree-forms in the family and most taxa are tropical, it is unlikely that fossil woods will be discovered. Investigations of fossil pollen

appear to be the most promising avenue for historical documentation of Acanthaceae.

The family is of little economic importance. A few plants have been reported to have medicinal properties, but none is included in modern works on materia medica. Bremekamp pointed out that the leaves of two new species of the Indonesian genus *Filetia* contain inulin, a carbohydrate not previously found in the family. Burkart listed a number of species, notably *Justicia campestris* Griseb., that can be used for emergency forage. Metcalfe & Chalk reported that blue dyes have been obtained from *Strobilanthes* species and yellow dyes from *Justicia* species, but they apparently have no economic value. The family is best known horticulturally for its many unusual and interesting ornamental plants that occur in the tropics.

Because of their tropical nature, it is not surprising that the Acanthaceae of the southeastern United States reach their best development in Florida. Some genera only reach southern Florida, and others, such as *Justicia* and *Ruellia*, are best represented in the United States within the state boundaries. Other genera represented in Florida, such as *Barleria* and *Hemigraphis*, are apparently not well established outside of cultivation, and still others are found only in gardens. *Andrographis* has been reported as occurring on chrome ore piles in Virginia but probably is not established in our flora. These three genera are included in the key unnumbered and in brackets.

Cultivated members of the Acanthaceae in the southeastern United States, particularly in Florida, include *Acanthus montanus* T. Anders. (leaves spiny); *Aphelandra tetragona* (Vahl) Nees (scarlet corollas, hooded upper lobes); *Crossandra infundibuliformis* (L.) Nees (bright scarlet-orange corollas); *Eranthemum pulchellum* Andr. (*E. nervosum* (Vahl) R. Br. ex Roem. & Schult.) (blue curved corollas); *Fittonia Verschaffeltii* E. Coem. (creeping herb; leaves white or red veined); *Graptophyllum pictum* Griff. (shrubs, leaves variously marked, corollas purplish or red, two lipped); various species of *Jacobinia* that resemble *Justicia* (brightly colored two-lipped corollas, inflorescences various); *Odontonema strictum* Kuntze (corollas bright red, flowers in close racemes); *Pachystachys coccinea* (Aubl.) Nees (*Jacobinia coccinea* (Aubl.) Hiern) (shrub with dense heads of scarlet flowers); *Peristrophe speciosa* (Roxb.) Nees (herb, flowers violet, subtended by two large bracts); *Pseuderanthemum atropurpureum* (Bull ex De Vos) Radlk. (leaves purplish or yellow blotched); *Sanchezia nobilis* Hook. f. (corollas yellow, with yellow revolute rims); and *Strobilanthes Dyeriana* Mast. (*Perilepta Dyeriana* (Mast.) Bremek.) (distinctive rose-purplish foliage).

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KEY TO THE GENERA OF ACANTHACEAE IN THE SOUTHEASTERN UNITED STATES

A. Retinacula papilliform or absent; herbs [shrubs] or vines without cystoliths; anthers 2-loculate; fruit a beaked or cuspidate capsule; seeds 4 to many.
  B. Vines; ovules 2 in each locule; calyx [annular or] toothed; stamens 4[or 2], basal lobes of anther spurred or blunt; capsule beaked; pollen spheroidal, spirotreme (subfam. Thunbergioideae). .... 1. *Thunbergia.*
  B. Erect herbs; ovules numerous in each locule; calyx more or less equally 5-parted; stamens 2, basal lobes of anther blunt; capsule beaked or cuspidate; pollen 3-colpate, syncolpate, prolate (subfam. Nelsonioideae). ..... 2. *Elytraria.*

A. Retinacula hooklike, subulate, truncate or more or less fimbriate at tip; herbs with or without cystoliths; anthers 1- or 2-loculate; fruit not beaked; seeds 2 to many.
  C. Shoots not articulated; cystoliths absent; stamens 4, anthers 1-loculate; pollen colpate (subfam. Acanthoideae). ..... 3. *Stenandrium.*
  C. Shoots articulated; cystoliths present; stamens 2 or 4, if 4 then at least 2 provided with 2-loculate anthers; pollen colporate or porate (subfam. Ruellioideae).
    D. Aestivation of corolla contorted; stamens usually 4; corolla actinomorphic, subactinomorphic or zygomorphic.
      E. Calyx actinomorphic or nearly so; stamens didynamous; inflorescence various.

F. Corolla limb actinomorphic or nearly so; capsule stipitate.
G. Inflorescence spiciform; bracts large, closely imbricate; corollas not projecting beyond the bracts. . . 4. *Blechum*.
G. Inflorescence axillary, or axillary and terminal, cymose, racemose, or paniculate, rarely in heads; bracts usually small, rarely imbricate; corollas projecting well beyond the bracts.
H. Calyx lobes lanceolate or linear; anther sacs blunt; corolla limb actinomorphic or subactinomorphic. . . . . 5. *Ruellia*.
H. Calyx lobes bristle-like; anther sacs awned or pointed at the base; corolla limb subactinomorphic. . . . . 6. *Dyschoriste*.
F. Corolla zygomorphic, bilabiate; capsule cylindrical, not stipitate.
I. Inflorescence racemose; stamens united in a short tube; 2 fascicles or rows of hairs present on posterior of the corolla. . . . . [*Hemigraphis*].
I. Inflorescence axillary, clustered, or flowers apparently solitary; stamens didynamous; corolla without hairs. . . . . 7. *Hygrophila*.
E. Calyx zygomorphic, the segments very dissimilar, posterior one usually largest, anterior pair more or less united; stamens not didynamous; inflorescence a dense terminal spike. . . [*Barleria*].
D. Aestivation of corolla cochlear; stamens 2 or 4; corolla zygomorphic, usually strongly bilabiate.
J. Ovules six or more in each locule; capsule not stipitate. . . . . [*Andrographis*].
J. Ovules two in each locule; capsule more or less distinctly stipitate.
K. Stamens 4. . . . . 8. *Asystasia*.
K. Stamens 2.
L. Stems 6-angled; calyx subtended by two partially united bracts; placenta separating from the mature capsule valves. . . . . 9. *Dicliptera*.
L. Stems subterete or slightly quadrangular; bracts distinct; placenta remaining attached to the valves of the capsule. . . . . 10. *Justicia*.

Subfam. THUNBERGIOIDEAE Lindau

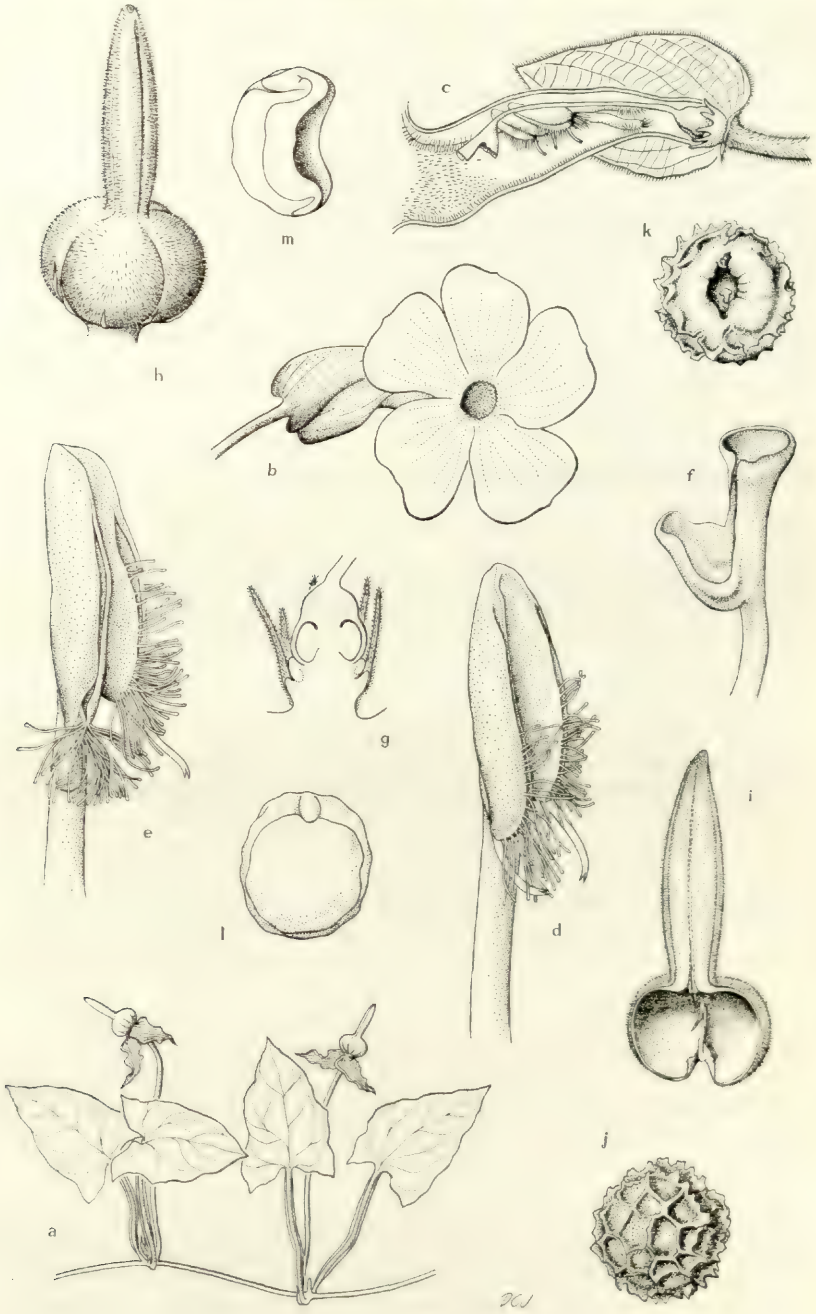
1. **Thunbergia** Retzius, Physiogr. Sällsk. Handl. 1(3): 163. 1776, nom. cons.

Climbing, often twining herbaceous [or woody] vines [or shrubs] with articulated stems. Leaves prevailingly sagittate, hastate, or cordate at the base. Flowers large, pedunculate, solitary in the axils [or in racemes, rarely cymose]; subtending bracts 2, spathaceous, large. Calyx persistent [variously reduced or shortly cupuliform, truncate] or 5–16-lobed. Corolla subactinomorphic to slightly zygomorphic, large, funnelform or salverform, tube slender, short, curved or straight, enlarged into a spreading 5-lobed

limb. Stamens didynamous, attached near the base of the tube; anthers with an apiculate connective, appendaged at base; pollen large, mostly 85–100μ in diameter, spirotreme, spheroidal. Disc present, fleshy. Stigma infundibular or peculiarly 2-lobed (see FIG. 1f); ovary fleshy, ovules 2 in each locule, funiculus pulvinate. Capsule rounded, coriaceous, abruptly flat-beaked, subtended by persistent bracts, loculicidally dehiscent; seeds 2 in each valve. Seeds semiglobose, with a conspicuous excavation on the inner side; retinacula none. (Not *Thunbergia* Montin, Vet. Akad. Handl. Stockholm **34**: 288. *pl. 11.* 1773, nom. rejic. = *Gardenia* Ellis [Rubiaceae].) TYPE SPECIES: *T. capensis* Retz. (Named for Carl Pehr Thunberg, 1743–1822, Swedish student and successor to Linnaeus, who traveled in Japan and South Africa and wrote floras of these regions, later professor of botany at Uppsala.) — CLOCK-VINE.

About 200 species of the Old World tropics, with 12 or more occurring in the American tropics and subtropics in cultivation or more or less naturalized, two of these in peninsular Florida. *Thunbergia alata* Bojer ex Sims, $2n = 18$, a slender, herbaceous vine with winged petioles and pale yellow to orange corollas, usually with a dark-purple "eye," is locally abundant along roadsides in moist thickets and near abandoned homesites southward from Brevard and Sarasota counties, Florida. It is a native of East Africa but is now thoroughly naturalized in many tropical areas. None of the Florida specimens has the rusty-villous pubescence found on younger stems and leaves of many specimens from the West Indies. Bremekamp (1948) formally described several new varieties in *T. alata* in Java based on degrees of pubescence of stems and leaves, but they hardly appear worthy of taxonomic recognition. The Indo-Malayan *T. fragrans* Roxb. (*T. volubilis* Pers.), also a smooth, herbaceous vine with usually hastate leaves but with white corollas, has been collected in hammocks along the Indian River, Brevard County, Florida. A number of varieties, again based on pubescence and on leaf shape, have been recognized in this species by both Nees and Clarke. *Thunbergia grandiflora* Roxb., $2n = 28, 56$, an herbaceous or somewhat woody twining vine with large, bright-blue to white, more or less campanulate corollas, a native of India, is cultivated in southern Florida and may persist after cultivation, but apparently has not become established as an escape. All three species belong to sect. THUNBERGIA (§ *Euthunbergia* Benth.

FIG. 1. **Thunbergia.** a–m, *T. alata*: a, portion of vine with nearly mature fruits, × ½; b, flower, × 1½; c. same in partial section, corolla lobes not shown, one bract removed, calyx and disc intact, to show relative positions of stamens and gynoecium, × 3; d, outer stamen, × 12; e, inner stamen, × 12; f, stigma, × 12; g, ovary, disc, and calyx in section cut to show placentation of two of four ovules, × 8; h, mature fruit before dehiscence, × 3; i, inner surface of valve of capsule after dehiscence, × 3; j, seed, abaxial surface, × 6; k. same, adaxial surface, × 6; l, embryo, abaxial surface — note radicle and position of cotyledons, × 6; m, same, in vertical section, adaxial surface to right — note radicle, plumule, and folding of cotyledons, × 6.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& Hook.) on account of their two-lobed stigmas and solitary axillary flowers.

The remarkable anatomy of *Thunbergia* has occasioned studies by Chodat, Roulet, and Mullenders. Interxylary phloem is produced directly from the inner surface of an otherwise normal cambium in *T. mysorensis* T. Anders. (sect. HEXACENTRIS (Nees) Benth. & Hook.) and in *T. grandiflora*. This "centrifugal" phloem is produced independently of the other secondary tissue. Also, xylem bridges that differentiate in a tangential fashion occur in normal phloem tissue. The presence of medullary xylem in a number of species is similar to that found in *Mendoncia*.

Roulet also investigated certain intrageneric relationships from an anatomical comparison of the stem and the morphology of pollen. He concluded that *T. fragrans* and *T. alata* are not closely related, but rather that *T. fragrans* is more closely allied with the African *T. hastata*, *T. capensis*, and *T. hirta*; *T. alata* is related to *T. reticulata* and *T. annua*, of East Africa.

Some interesting observations have been made regarding the reproductive biology of *Thunbergia*. Cammerloher (see also Faegri & Van der Pijl) reported that the extra-floral nectaries of *T. grandiflora* function as part of the pollination system. Certain carpenter bees, such as *Xylocopa aestuans* and *X. latipes*, have been observed as pollinators of this species. The bee must crawl into the corolla tube and in so doing pushes against the stigma. The stigma and anthers are in an expanded outer chamber of the tube, while a constriction in the tube separates this from a small inner chamber that incloses the ovary and nectary. The thick wall of the tube at the constriction prevents tearing of the corolla and blocks passage of the insect. A narrow channel runs down to the nectary alongside the style, and the insect must extend its tongue along this to reach the nectar. Hairs attached to the anthers are touched by the insect and this results in the anthers being pulled down on its back, which is dusted with pollen. *Xylocopa* bees are often nectar "thieves" and from the outside will chew a hole through the base of the corolla thereby obtaining access to the nectar. This "illegitimate" circumvention of the pollinating mechanism is prevented, however, by ants attracted to the extrafloral nectaries on the bracts, pedicel, and calyx. If another insect, such as a *Xylocopa*, is similarly attracted by the extrafloral nectar, the ants aggressively chase it away. Flowers lacking these nectaries almost invariably have corollas with holes in their bases. Various other floral adaptations to insect pollination have been reported for *T. alata* and *T. erecta* (Benth.) T. Anders. by Knuth.

Cytological studies in *Thunbergia* point to the widespread occurrence of polyploidy. Mangenot & Mangenot have reported $2n = 32$, 48, and 64 for three species, which suggests a base number of $x = 8$. Other numbers reported for the genus ($2n = 18$, 28) may have resulted through aneuploidy. Additional counts would be important in *Thunbergia*, but the available evidence already suggests that variation in chromosome number has been important in speciation within the genus.

The classification of plants related to *Thunbergia* has been a matter of long-standing controversy. Nees (1847) maintained *Thunbergia*, *Meyenia* Nees, and *Hexacentris* Nees as separate genera. Anderson, however, did not, and later Bentham & Hooker treated the three as sections of an inclusive *Thunbergia*. Radlkofer suggested on the basis of pollen and anatomical characters restoration of *Meyenia* to generic rank. He was followed by Lindau (1893), who treated *Thunbergia*, *Meyenia*, and *Pseudocalyx* as constituting subfam. Thunbergioideae, while placing the tropical American *Mendoncia* in a separate subfamily, Mendoncioideae, on the basis of its drupaceous fruit, absence of retinacula, and pollen morphology. (Lindau's is the most recent review of *Thunbergia* in its entirety. In it he established four sections based on the morphology of the stigma and the inflorescence.) Roulet (1894), after a detailed anatomical study, concluded that the three genera could not be maintained separately. Van Tieghem, however, disagreed and, stressing pollen, anther dehiscence, and petiolar anatomy, restored *Hexacentris* to generic rank and concurred with Radlkofer and Lindau in maintaining *Meyenia* as distinct from *Thunbergia*.

Bremekamp initially accepted the inclusion of *Thunbergia* in the Acanthaceae but later (1953) decided to follow Van Tieghem (1908; see under Family References), who had proposed the establishment of a separate family, Thunbergiacées, on the basis of the rostrate capsule and distinctive excavation on the ventral side of the seeds. Bremekamp thought *Thunbergia* to be more closely related to Mendoncioideae, Bignoniaceae, and Pedaliaceae than to Acanthaceae. Both Lindau and Bremekamp attached great taxonomic significance to pollen types in their classification of *Thunbergia*, and Raj concurred with Bremekamp that Thunbergioideae ought to be raised to family status on the basis of pollen characters. He also recommended that *Meyenia* be excluded from the family and transferred to the Pedaliaceae, again on the basis of pollen characters. It appears obvious that the uncertainty of the relationships of *Thunbergia* cannot be removed by conventional taxonomic approaches. Additional information derived from cytogenetical and chemotaxonomic techniques is very desirable for this genus.

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Subfam. NELSONIOIDEAE Lindau

2. **Elytraria** Michaux, Fl. Bor.-Am. 1: 8. 1803, nom. cons.

Acaulescent [or caulescent] rigid herbs with basal rosettes. Leaves alternate or sometimes subopposite, basal [or crowded at the ends of branches]. Flowers borne in dense, scapose, terminal spikes, peduncles and inflorescence bearing imbricate, coriaceous bracts; bracteoles subtending calyx somewhat shorter than the calyx. Calyx 4-parted, scarious, segments narrow, dentate or entire at the apex. Corolla blue or white, tube cylindrical, limb slightly bilabiate, lower lip 3-lobed. Stamens 2, barely

exserted, anthers sometimes awn-tipped at the base, 2-loculate, locules equal, parallel; staminodia usually absent; pollen 3-colpate, syncolpate, prolate, about 30 × 40 μ in diameter, shed at the 2-celled stage. Ovary 2-loculate, placentation parietal, ovules 6–10 in each locule, amphitropous, funicular obturator and retinaculum absent. Capsule narrow, acute at apex, contracted at base, thick-walled, with explosive dehiscence. Seeds more or less flattened; embryo spatulate, slightly bent; endosperm present, ruminate. Embryo sac with persistent antipodal cells, often becoming binucleate; endosperm cellular, conforming to the Pedicularis type; embryogeny conforming to Lythrum-variation of Onagrad type. (*Tubiflora* J. F. Gmel., nom. rejic.) TYPE SPECIES: *E. virgata* Michx., nom. illeg. = *E. caroliniensis* (J. F. Gmel.) Pers. (Name derived from Greek *elytron*, sheath, referring to the coriaceous bracts that cover the scapes and subtend the flowers.)

A small genus of perhaps 15 species in the tropics and subtropics of both Old and New worlds. The American species were treated by Leonard, who recognized twelve species in the Western Hemisphere. In our flora the genus is represented by *Elytraria caroliniensis* (J. F. Gmel.) Pers. var. *caroliniensis* (*E. virgata* Michx., *Tubiflora caroliniensis* [Walt.] J. F. Gmel.), which occurs on the Coastal Plain from southern South Carolina to southern peninsular Florida (Lee County), where it is locally abundant in bottomlands, wet pine barrens, and in calcareous gravel. It is a well-marked species with large, basal leaves in a rosette, and a stout, virgate scape with one or more spikes. In southern Florida (Collier and Dade counties) a narrow-leaved form, *E. caroliniensis* var. *angustifolia* (Fern.) Blake (*Tubiflora angustifolia* (Fern.) Small) is sometimes frequent locally, also in wet or rocky soil. Beyond our range, *E. bromoides* Oerst., a somewhat dwarf form that may prove to be a geographic subspecies of the *E. caroliniensis* complex, occurs in Texas.

The taxonomic position of *Elytraria* and that of the Nelsonioideae have been controversial since St. Hilaire first included the genus in the Acanthaceae (1805). Sprengel, for one, did not accept this decision and transferred the genus to the Scrophulariaceae (1817), a course also followed by Link (1821). Lindley (1847) placed *Elytraria* in his segregate family Nelsoniaceae. Lindau established the subfamily Nelsonioideae because, on the basis of the general habit of the plants, the presence of papilliform retinacula in a number of genera, and the presence of explosively dehiscent capsules, he believed the genera properly belong in the Acanthaceae. The Nelsonioideae, including five genera, three of them monotypic, is the largest of his first three subfamilies. After a detailed study of various groups of genera, Bremekamp (1953, 1965) proposed that the Nelsonioideae be transferred to the Scrophulariaceae "in the vicinity of the Rhinantheae." Earlier, however, Bhaduri had expressed the view that possibly the Nelsonioideae did not even deserve subfamily rank, since the pollen resembles that of *Acanthus* and *Crossandra*, of the Acanthoideae, and is not otherwise distinctive.

Johri & Singh challenged Bremekamp's views and after a detailed study of microsporogenesis, megagametogenesis, embryogeny, and endosperm formation concluded that *Elytraria* is in general conformity with other members of the Acanthaceae. The only feature of special interest is the formation of peripheral endosperm cells that form prominent ridges owing to unequal growth. This imparts an uneven or ruminate appearance to the structure, a feature uncommon in Acanthaceae. In an elaborate defense, Bremekamp (1965) emphasized the alternate leaves, parietal placentation, scapose habit, and type of endosperm in Nelsonioideae, all characters that tend to associate the group with Scrophulariaceae, particularly tribe Rhinantheae. He concluded that Johri & Singh did not prove that the Nelsonioideae belong with the Acanthaceae, although he not only ignored the embryological data, but also the pollen characters and the hemiparasitism of Rhinantheae, a characteristic unknown in Nelsonioideae. Morton has reported $2n = 38$ for three African species of *Elytraria*, suggesting a base number similar to that for other Acanthaceae. Martin described what he termed a "spatulate," slightly bent embryo in *Elytraria*, although the Acanthaceae generally produce non-spatulate, strongly bent embryos. Certainly the total evidence is equivocal, and one must conclude that the position of *Elytraria* and other Nelsonieae is uncertain at the present time. Probably no special advantages would accrue from a transfer to the Scrophulariaceae since other problems would then arise. Additional cytological information, as well as genetic and chemotaxonomic evidence, ought to shed light on the systematic position of the group.

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Subfam. ACANTHOIDEAE Lindau emend. Bremek.
Tribe APHELANDREAE Nees emend. Bremek.
Subtribe **Aphelandrinae** Bremek.

3. **Stenandrium** Nees in Lindley, Nat. Syst. Bot. ed. 2. 444. 1836, nom. cons.

Perennial acaulescent [caulescent or suffrutescent] herbs. Leaves entire, often radical. Flowers borne in scapose spikes [or subsessile or sessile, peduncles axillary, leafless], simple [or branched]; bracts herbaceous, imbricate, lanceolate to ovate, entire [sometimes dentate]; bracteoles

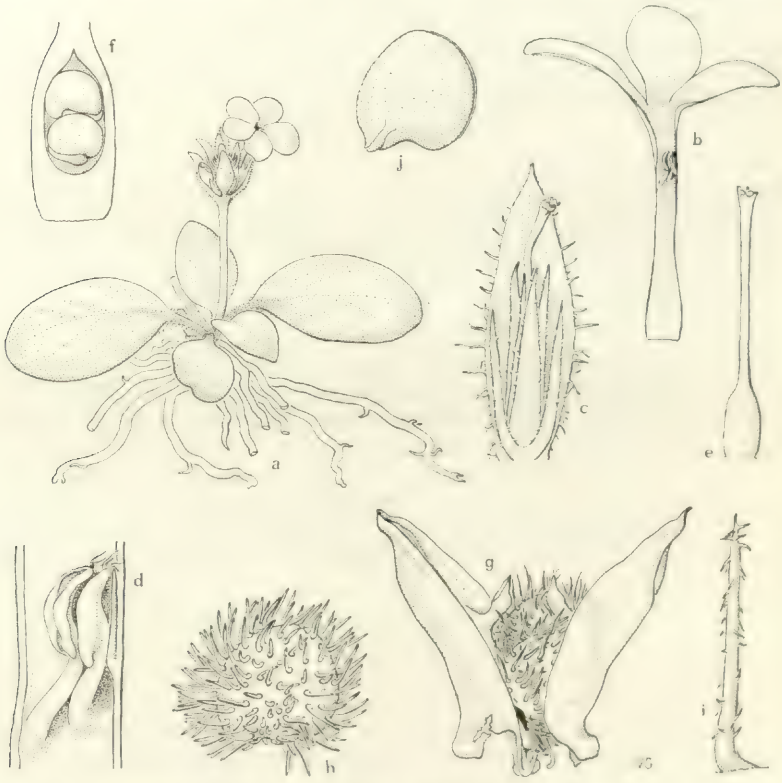

FIG. 2. **Stenandrium.** a–j, *S. dulce* var. *floridanum*: a, flowering plant, × 1; b, corolla in vertical section to show position of stamens and staminodium, × 3; c, flower with bract and two bracteoles, corolla removed, × 4; d, portion of corolla tube in vertical section showing two of four stamens and staminodium, × 15; e, gynoecium, × 6; f, ovary in vertical section to show septum and two ovules, × 15; g, open capsule with two of four seeds retained — note retinacula above, × 4; h, seed with echinate seed coat, after moistening, × 5; i, single spine-like hygroscopic hair from seed coat, after moistening, × 25; j, embryo, moistened, oriented as in seed (h), × 5.

subtending calyx short, setaceous. Calyx lobes 5, subequal, narrow, acute, striate-nerved. Corolla infundibuliform, pinkish, purple [or white], tube cylindrical, slender, somewhat oblique and slightly enlarged at the throat, limb [4- or] 5-lobed, spreading, lobes rounded, subequal, retuse or obovate, imbricate. Stamens didynamous, adnate in the throat of the tube, included; filaments very short; anthers 1-loculate, linear, connivent or almost cohering in pairs, muticous at base; pollen variable, spheroidal, with indistinct apertures [or 3-colpate, prolate, reticulate or anomotreme, pantoporate]. Disc inconspicuous, truncate. Style filiform, stigma subclavate, obconical, simple or obscurely 2-lobed; ovules 2 in each locule. Capsule subfusiform, oblong to subterete; seeds 4, or sometimes fewer by abortion, orbicular, plano-compressed, minutely muricate, echinate [to hispid], each subtended by a long retinaculum. (*Gerardia* L., nom. rejic.) LECTOTYPE SPECIES: *S. mandioccanum* Nees. (Name from Greek *stenos*, narrow, and *andros*, male, referring to the narrow anthers characteristic of the Aphelandreae.)

A genus of remarkable distribution with perhaps 30 species, all in tropical and subtropical regions of the Western Hemisphere, except for one that is endemic to Madagascar. Our representative is *S. dulce* (Cav.) Nees var. *floridanum* Gray (*S. floridanum* (Gray) Small, *Gerardia floridana* (Gray) Small), an inconspicuous, uncommon, low herb of seasonally wet pinelands, moist sandy soil, and grassy roadsides of southern peninsular Florida, from Citrus and Osceola counties south into the Florida Keys. Our plants are very similar in appearance to the highly variable var. *dulce*, which ranges from southern Chile to Mexico; they differ chiefly in usually having upper bracts and bracteoles glabrous or sparingly hirsute-ciliate, rather than hirsute. They are highly variable in pubescence and in leaf morphology, the blades varying from narrowly spatulate to suborbicular. Individual plants may be from 4–6 cm. to 15 cm. tall. Superficially, *S. dulce* var. *floridanum* also appears to be related to the Mexican *S. subcordatum* Standl., of Yucatan, and to *S. mexicanum* Leonard. Other Mexican plants, such as *S. fasciculare* (Benth.) Wasshausen may also be elements of the *S. dulce* complex. Our plants do not, however, appear to be closely related to *S. barbatum* Torr. & Gray, a very hirsute, many-stemmed plant with numerous, crowded leaves, which occurs in Texas and New Mexico.

The relationships of the genus are apparently with other tropical American Aphelandrinae. Nees (1847) thought *Stenandrium* to be nearest *Crossandra*. He divided the 16 species into two informal groups, "Acaulia vel subacaulia . . ." and "Caulescentes . . . ." Strangely, Bentham & Hooker placed the genus in the tribe Justicieae, subtribe Asystasiinae, among genera to which it bears no relation. Lindau followed Nees in placing *Stenandrium* in Aphelandreae; his classification suggested intergeneric relationships with the monotypic Central American *Strobilacanthus* Griseb. and with the large tropical American genus *Aphelandra* R. Br. Lindau recognized two unequal sections, sect. STENANDRIUM

(§ *Schizostenandrium* Lindau) and sect. SPHAEROSTENANDRIUM Lindau, based entirely on differences in pollen morphology. Our species would be placed in the latter. The present subgeneric disposition of species must be considered unsatisfactory, since one species, the Brazilian *S. trinerve* Nees, has one variety in one section, another variety in the other! Bremekamp initially placed the genus in Acantheae (1948) but later returned it to the Aphelandreae (1965).

Stenandrium is one of several genera of Acanthaceae that exhibit a wide range of pollen types. Raj found that the pollen of *S. barbatum* was 3-colpate, goniotreme, prolate; that of *S. trinerve* anomotreme, spheroidal; that of *S. Pohlii* Nees (Brazil) 6–7-porate, spheroidal; and that of *S. droseroides* Nees 3-colpate, prolate, with finely reticulate sculpturing. Pollen-grain size, however, was fairly uniform. With this much variation in pollen morphology it appears that pollen characters are not a sound basis for future monographic revision.

Chromosome counts are highly desirable, since not a single species of *Stenandrium* has been reported on cytologically.

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———. A new *Stenandrium* from the State of Durango, Mexico. *Ibid.* 83–85. [*S. pelorium* Leonard, an unusually large sp.]

STANDLEY, P. C. Three new plants from Yucatan. Jour. Arnold Arb. **11**: 47, 48. 1930. [Includes *S. subcordatum* Standl.]

THIERET, J. W. Proposal for the conservation of the generic name *Stenandrium* Nees versus *Gerardia* L. (Acanthaceae). Taxon **5**: 58. 1956.

Subfam. RUELLIOIDEAE Bremek.

Tribe RUELLIEAE Nees emend. Bremek.

The Ruellieae as redefined by Bremekamp (1944) and Bremekamp & Nannenga-Bremekamp (1948) is a large tribe composed of several subtribes, none of which is precisely delimited. They all, however, are characterized by usually contorted aestivation of the corolla lobes, by spheroidal or ellipsoidal, 3- or more-porate pollen grains, and by reticulate, spinulose, or banded pollen surfaces. Lindau's tribes Hygrophileae, Petalidieae, Strobilantheae, and Barlerieae, are retained as subtribes with considerable emendation by Bremekamp; they are distinguished largely on the basis of differences in pollen morphology. The descriptive anatomy of several genera of Ruellieae showing comparative relationships was reported by Tchouproff.

Subtribe **Blechinae** Bremek.

4. **Blechum** P. Browne, Civ. Nat. Hist. Jamaica 261. 1756.

Perennial herbs. Leaves petiolate, entire, repand, dentate or crenate. Flowers small, sessile or on very short pedicels in the axils of bracts; inflorescence a more or less dense, terminal [or axillary] spike or spiciform raceme; bracts imbricate, ciliate, broad, suborbicular [or elongate]. Calyx deeply 5-parted, segments linear-subulate, nearly equal [or unequal, almost bilabiate]. Corolla infundibuliform, white or purplish; tube elongate, slender; limb short, nearly equally 5-lobed, contorted in aestivation, barely or not extending beyond the subtending bracts of the flower. Stamens didynamous, included, adnate about the middle of the tube; anthers 2-loculate, muticous, locules parallel; pollen 3-colporate, syncolporate, spheroidal, about 47 μ in diameter. Style filiform; stigma subulate, obscurely lobed, the posterior lobe minute; ovules few to 6 in each locule. Capsule broadly oblong [ovoid or orbicular], with a short, narrow base. Seeds suborbicular, plano-compressed, surface with mucilaginous hairs when moistened; supporting retinacula acute; septum breaking away in the mature capsule. TYPE SPECIES: *Ruellia Blechum* L. = *Blechum Brownei* Juss. (Apparently a Greek name for wild pennyroyal, *Mentha Pulegium* L.)

Blechum is a small genus of ten or possibly fewer species of herbs indigenous to the American tropics; one species has been introduced into the Old World tropics as a weed and is now rather common in warm climates of the world. In general, the genus is recognized by its dense, sometimes 4-sided spike, very reduced flowers, and the mature capsules in which the septum breaks away from the capsule wall. Our single representative is *B. Brownei* (*B. pyramidatum* (Lam.) Urban; cf. Bremekamp, 1938, p. 149), $2n = 34$, which occurs as an occasional naturalized weed in extreme southern Florida, usually in damp soil and in the margins of mangrove areas (*Lakela 26876*, GH, USF). The species can be easily recognized by its dense, conspicuously bracteate, 4-sided spikes and small flowers. It is widely distributed throughout the American tropical regions in open cultivated or waste places, in both dry and moist soil, from eastern and southern Mexico through Central America and the West Indies to northern South America. It has been introduced as a weed in the Old World tropics.

The intergeneric relationships of *Blechum* are uncertain. Nees (1847) placed the genus in his subtribe Diclipteae, believing it to be allied to *Dicliptera* and *Rungia* on the basis of the detachable septa in mature capsules of all three genera. Nees's reference to the occurrence of *Blechum* in Madagascar and the East Indies is unclear, since he does not record any of the eight species described as having been found there. Bentham & Hooker placed the genus in the subtribe Petalidiinae, while recognizing that its three to many ovules per locule made it dissimilar to other genera

in the group. Lindau classified *Blechum* in his tribe Petalidieae together with four other genera, but Bremekamp & Nannenga-Bremekamp (1948) removed it to a subtribe of its own because of its racemose inflorescence and peculiar pollen. It should also be pointed out that they stated that the separation of Petalidiinae, Blechinae, and Ruelliinae is based only on differences in the morphology of pollen. Melchior has gone a step farther and recognized the tribe Blecheae (including only *Blechum*) and has placed it near the Barlerieae.

Grant reported that *Blechum Brownei* has 34 somatic chromosomes, as does *Ruellia*, and said that karyology and chromosome number indicated affinity of the two genera and provided little evidence for their separation. Satellite chromosomes were observed in both genera, with the satellites attached by a slender thread to the short arm of a chromosome with a subterminal centromere. He suggested that *Blechum* may have been derived by hybridization of plants with basic chromosome numbers of $x = 8$ and $x = 9$. Leonard (1951) also emphasized the similarity of *Blechum* and *Ruellia*, pointing out that the only conclusive difference between the two is the breaking away of the septum from the mature capsule in *Blechum*, while it remains intact in *Ruellia*. The type species of *Blechum* was first thought to be a *Ruellia* because of its close morphological similarity to that genus.

Oersted recognized in *Blechum* two subgenera based on morphology of the calyx and bracts, Blechum (subg. *Eublechum* Oerst.) and Chiloblechum, which were treated as sections by Lindau (1895) with the species about equally divided between the two. In his treatment of Acanthaceae of the West Indies Lindau (1900) recognized three species of *Blechum*, with the others restricted to Central America and Mexico, but both sections are represented over the range of the genus.

References:

Under family references see Baillon (p. 433), Bentham & Hooker, Bremekamp & Nannenga-Bremekamp (1948), Grant, Leonard (1951), Lindau (1895), Melchior, Nees (1847), and Raj.

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Oersted, A. S. Mexicos og Centralamerikas acanthaceer. Vidensk. Medd. Naturl. For. Kjøbenhavn **6**: 113–181. 1854. [Subg. *Chiloblechum*.]

Subtribe **Ruelliinae** Bremek.

5. **Ruellia** Linnaeus, Sp. Pl. 2: 634. 1753; Gen. Pl. ed. 5. 238. 1754.

Perennial caulescent herbs [or shrubs], usually pubescent. Leaves sessile or petioled, mainly entire, undulate [rarely dentate]. Flowers large

and showy (usually), or small and cleistogamous, solitary, or more often clustered in the leaf axils, or borne in terminal or axillary cymes or cymose panicles; bracteoles sessile or subsessile, narrow, small [or sometimes oblong to lanceolate, herbaceous, imbricate, and conspicuous]. Calyx deeply 5-parted or cleft, the segments linear or narrow, acute, subequal [or posterior lobe larger, or 2-lipped]. Corolla infundibuliform, purple, lavender, white [red, rose, or yellow], sometimes saccate; tube short to long (sometimes quite long), narrow below, straight or oblique; limb of 5 obtuse, spreading lobes, nearly regular [or 2 posterior lobes connate at the base forming a lip], aestivation convolute; cleistogamous flowers with corolla small, tubular, closed. Stamens 4, rarely 5, didynamous, adnate below the throat, included [or exserted]; anthers parallel, 2-loculate, oblong-sagittate, muticous; filaments dilated at the base, anterior filaments larger; pollen 3-porate, spheroidal, from 47 to 99 μ in diameter. Disc inconspicuous [or frequently conspicuous]. Style slender, usually slightly recurved at apex; stigma simple, subulate or 2-lobed, the lobes equal or posterior lobe short or obsolete; ovules 2–10 in each locule, anatropous. Capsules linear-oblong, narrow, or clavate, somewhat flattened, base very short or contracted into a solid, elongate stipe. Seeds 4–20, plano-compressed, suborbicular, with a mucilaginous coat that exhibits, after moistening, tapered, short hairs with walls marked internally by rings or spirals; retinacula elongate, acicular, hooked. $2n = 34$. (Including *Aphragmia* Nees in Lindl., *Arrhostoxylum* Nees in Mart., *Cryphiacanthus* Nees, *Dipteracanthus* Nees.) LECTOTYPE SPECIES: *Ruellia tuberosa* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 3: 241. 1913. (Named in honor of Jean de la Ruelle, 1474–1537, a French physician and herbalist.)

The second largest genus of Acanthaceae with about 250 species distributed throughout the tropics and subtropics; relatively few species in the temperate regions of North America; six indigenous species and three introductions in the southeastern United States. The genus has an interesting quadricentric distribution that corresponds in general to that for the family, with centers of variation in Brazil, Indo-Malaya, Central America, and Africa. The circumscription of *Ruellia* adopted here is essentially that of Lindau (1895). The genus has long been recognized as taxonomically very difficult, and Lindau freely admitted that his intrageneric classification was tentative.

Our most important species is the polymorphic *Ruellia caroliniensis* (J. F. Gmel.) Steud. subsp. *caroliniensis*, *sensu stricto* (*R. hybrida* Pursh, *R. parviflora* sensu Small), which occurs throughout the Southeastern States in a wide variety of habitats, such as bottomlands, sandy woods, limestone soils, old fields, disturbed sites, scrub vegetation, etc. Fernald described six varieties, in addition to the typical one, and five forms, primarily on the basis of slight differences in leaf shape and on pubescence patterns. These appear to be of doubtful taxonomic value, since they describe minor variations induced by environmental modification or by small genetic differences. In southern peninsular Florida occurs an en-

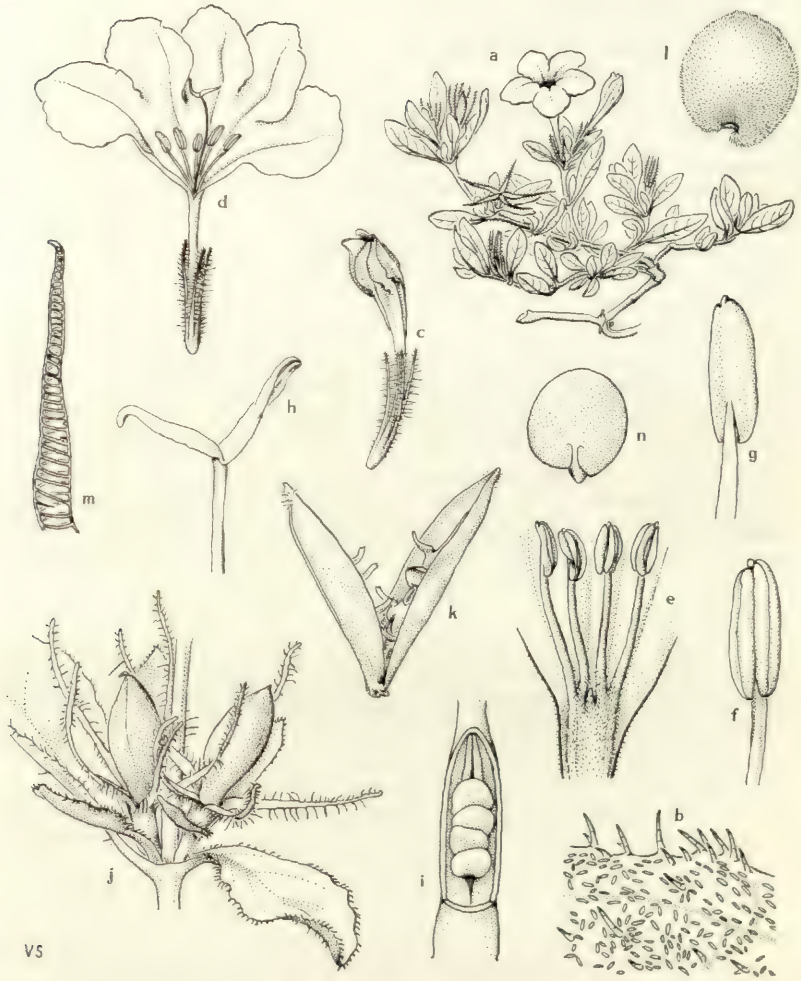

FIG. 3. **Ruellia.** a–j, *R. caroliniensis* var. *heteromorpha*: a, flowering and fruiting branch, × ½; b, portion of leaf, showing trichomes and cystoliths, × 12; c, flower bud, × 1; d, flower with five stamens, corolla partly laid open, × 1; e, androecium of flower with four stamens and staminodium, × 3; f, g, two views of anther, × 8; h, stigmata, × 8; i, ovary in partial section to show placentae and ovules of one locule, × 12; j, node with two nearly mature fruits, × 2. k–n, *R. humilis*: k, open capsule showing retinacula, one aborted seed remaining in right-hand valve, × 3; l, seed with covering of hygroscopic hairs, after moistening, × 6; m, small hair (about half as long as most) from seed coat, showing internal spiral and annular thickenings, × 200; n, embryo from moistened seed, × 6.

demic variety, *R. caroliniensis* subsp. *caroliniensis* var. *succulenta* (Small) R. W. Long[2] (*R. succulenta* Small), a distinctive ecotype generally restricted to the Everglades region. *Ruellia caroliniensis* subsp. *ciliosa* (Pursh) R. W. Long[3] is found in dry pinelands and scrub vegetation from South Carolina to central Florida, thence west to southeastern Louisiana. Hybrid populations of the two subspecies are frequent in northern and central Florida in disturbed sites. A second endemic variety, *R. caroliniensis* subsp. *ciliosa* var. *heteromorpha* (Fern.) R. W. Long,[4] occurs in sandy pinelands and in disturbed sites from Volusia and Lee counties, Florida, south into the Keys. Hybrid populations of the two endemic varieties are not uncommon in southern Florida.

Fernald also described a number of new but doubtfully important varieties in *R. humilis* Nutt., a highly variable species that is found only in the western part of our area, in open fields, dry prairies, and rocky soil from Iowa and Kansas south to Texas, extending into western Virginia, Tennessee, Alabama, and western Florida. Some introgression between *R. humilis* and *R. caroliniensis* occurs in their area of overlapping distribution. *Ruellia noctiflora* (Nees) Gray is endemic to wet pinelands and savannahs from southwestern Louisiana to northern Florida and eastern Georgia; it is one of our most distinctive species because of its elongate corolla tube and capsule. Genetic evidence (Long, unpublished) indicates that it is related to the *R. humilis* complex. The Ozarkian *R. pedunculata* Torr. ex Gray subsp. *pedunculata* extends from southern Illinois south into western Louisiana, eastern Texas, and eastern Oklahoma in calcareous or rocky soils. A disjunct subspecies, *R. pedunculata* subsp. *pinetorum* (Fern.) R. W. Long,[5] a smaller and smoother form but with the characteristic elongate peduncles of subsp. *pedunculata*, occurs in low pinelands of South Carolina, northern Florida, and Louisiana. *Ruellia strepens* L. (including *R. strepens* f. *cleistantha* (Gray) McCoy) reaches its greatest development in the Mississippi basin and adjacent areas and extends into the Carolinas and Virginia, principally in bottomlands and on calcareous soils. A related taxon, *R. Purshiana* Fern. (including *R. Purshiana* f. *claustroflora* Fern.), is endemic to the mountainous

[2] **Ruellia caroliniensis** subsp. **caroliniensis** var. **succulenta** (Small) R. W. Long, stat. nov.
R. succulenta Small, Bull. N.Y. Bot. Gard. **3**: 437. 1905.

[3] **Ruellia caroliniensis** subsp. **ciliosa** (Pursh) R. W. Long, stat. nov.
R. ciliosa Pursh, Fl. Am. Sept. **2**: 420. 1814.
Dipteracanthus ciliosus (Pursh) Nees, Linnaea **16**: 204. 1842.
R. humilis sensu Small, Fl. Southeast. U.S. 1084. 1903, and Man. Southeast. Fl., 1933, non Nutt.

[4] **Ruellia caroliniensis** subsp. **ciliosa** (Pursh) R. W. Long var. **heteromorpha** (Fern.) R. W. Long, stat. nov.
R. heteromorpha Fernald, Rhodora **47**: 32. 1945.
R. hybrida sensu Small, Fl. Southeast. U.S. 1084. 1903, non Pursh, Fl. Am. Sept. **2**: 420. 1814.

[5] **Ruellia pedunculata** Torr. ex Gray subsp. **pinetorum** (Fern.) R. W. Long, stat. nov.
Ruellia pinetorum Fernald, Rhodora **47**: 24. 1945.

region and Piedmont plateau from western Maryland south to Alabama, in woods and on calcareous or acid soils. The morphology of the plant suggests that it may be of hybrid origin involving *R. strepens* and *R. caroliniensis*, although Uttal reported that the two species grow in adjacent areas and apparently do not hybridize. All these species represent sect. DIPTERACANTHUS (Nees) Lindau.

A second group of species in our flora has been introduced into Florida from tropical America. The Mexican and Antillean *R. Brittoniana* Leonard emend. Fern. (*R. malacosperma* sensu Small, non Greenman), of sect. PHYSIRUELLIA Lindau, has escaped from cultivation and is naturalized in waste areas and around former homesites in southern Florida, possibly in Louisiana, and also in Texas. A single collection of *R. malacosperma* Greenm., of sect. RUELLIA, from Key West, Florida, indicates that this plant is locally escaped. Apparently *R. Lorenziana* Griseb., an Argentinian species of sect. RUELLIA related to *R. tuberosa* L., is a new addition to our flora that is locally naturalized near Homestead, Florida. Although Britton & Millspaugh in their *Bahama Flora* state that *R. tuberosa* occurs in the southern United States, no specimens of this common tropical weed have been seen from our area.

Ruellia is the only acanthaceous genus for which there is some information about interspecific relations as determined by hybridization tests. Probably one of the first interspecific hybrids was made by Müller, who successfully crossed two Brazilian species, *R. formosa* and *R. silvaccola*. Morphologically intermediate hybrids were produced by almost 50 per cent of the seeds formed from crossing experiments. Bowden reported a sterile hybrid, *R. ciliosa* (= *R. humilis* Nutt.?) × *R. tuberosa*. Long successfully crossed *R. caroliniensis* with *R. humilis* and suggested that natural hybridization may be a factor causing the observed intergradation of these species in their area of overlapping distribution. From a study of breeding systems in populations of southern Florida, he concluded that the four taxonomic species involved are ecological races of a single polytypic species, *R. caroliniensis*. An investigation of interspecific hybrids resulted in the production of 22 different F_1 hybrids involving 12 North American taxa. Intersectional crosses, such as *R. brittoniana* × *R. occidentalis*, produced partially or completely sterile but sometimes vigorous hybrids. Abnormal meiosis in these hybrids may account for the high sterility.

The breeding systems in both the eastern species and the Texan "paniculate" species centered on *R. nudiflora* involve showy, chasmogamous flowers and small, tubular, cleistogamous flowers. Chasmogamous flowers favor outcrossing both structurally and by regular proterogyny. Generally, cleistogamous flowers are produced more abundantly towards the end of the growing season in the eastern species (at the beginning, in the paniculate species) producing numerous fruits with good seeds. The total evidence suggests that local populations are predominantly autogamous, particularly in the northern portion of our range, but that outbreeding occurs frequently in populations from Florida.

Long concluded that no revision of the genus ought to be attempted

until a thorough investigation of the reproductive biology of *Ruellia* species has been completed. Genetic barriers to interspecific crossing are lacking between many species, although these same species have been placed in different genera by various authors (especially Bremekamp). If it can be assumed that crossability is correlated with evolutionary relationship, the broad generic interpretation of Lindau may be a more accurate reflection of the natural limits of *Ruellia* than the numerous segregate genera advocated by Bremekamp.

Embryo sac development and microsporogenesis have been studied by Mauritzon, Maheshwari & Negi, Narayanan, Mohan Ram, and Wall & Long. No walls form after the first reduction-division during pollen formation in *Dipteracanthus patulus*; quadripartition occurs by furrowing with tetrads decussate or isobilateral. The single-layered nucellus is completely absorbed by the time the four-nucleate stage of the embryo sac has been reached. Development of the embryo sac is of the Polygonum type, with the tip of the sac extending into the micropyle. Both synergids and antipodals are ephemeral, but pollen tubes persist, and remnants can be recognized even in mature seeds. The endosperm is of the cellular type and is composed of a two-nucleate micropylar haustorium, a four-nucleate chalazal haustorium, and a central chamber that later separates into a cellular upper portion and a free-nuclear lower portion. A notable feature is the occasional formation of twin embryos. Additional embryos may arise by the proliferation of some of the suspensor cells.

In an investigation to determine whether there are embryological differences between *Ruellia tuberosa* and *Dipteracanthus patulus*, Mohan Ram concluded that, in general, both show the same type of embryology, although twin embryos were not found in *R. tuberosa*. The only notable difference was the presence of a cellular basal apparatus, a structure apparently absent in *D. patulus*. Chromosome numbers may be different for the two genera, however. Kaur and De both report $2n = 44$ for *D. prostratus*; the somatic number for *R. tuberosa* is $2n = 34$. In any event, the investigations thus far in the genus clearly demonstrate the usefulness of experimental approaches to the definition of both genera and species. Hybridization tests may yet prove to be a more satisfactory means of defining natural groups than pollen characters or floral morphology within Ruelliinae.

The genus has little economic importance. A number of tropical species are popular cultivars, mostly in greenhouses. *Ruellia Devosiana* Morr. and *R. Makoyana* Hort. both have purplish leaves, usually with attractive white venation; the former has white corollas marked with purple or lilac, the latter bright reddish corollas. The bright-blue-flowered *R. squarrosa* Hort. is grown in southern Florida as a ground cover and rock garden plant.

Members of the subtribe Ruelliinae have pollen with three equatorial pores, or rarely four to seven evenly distributed pores, or "sparsiporous," alveolate, echinulate or granulate exines. In his key to the genera of Ruelliinae of the Malay Archipelago and New Guinea, Bremekamp included eight genera, four of which were included as synonyms by Lindau

in his treatment of *Ruellia*, and two of which are new. The recognition of segregates from *Ruellia* is based largely on inflorescence patterns, corolla morphology, and pollen sculpturing. For instance, *Ruellia* is said to differ from *Arrhostoxylum* in having pollen with smaller, shallower, more regular alveolae.

Ruellia was emended by Bremekamp and restricted to the four species centering on *R. tuberosa*, as treated by Leonard, but also including *R. malacosperma* Greenm., a circumscription coinciding with the original delimitation of *Cryphiacanthus* Nees. In contrast, Lindau (1895) used a broad, inclusive definition of *Ruellia*, including 19 segregate genera. He recognized nine sections (four monotypic) based on morphology of the capsule and the flower. His sect. RUELLIA is entirely American and corresponds with *Ruellia* L. emend. Bremek. His sect. DIPTERACANTHUS (Nees) Lindau corresponds in part to *Dipteracanthus* Nees emend. Bremek., although Bremekamp restricted the genus to paleotropic species with sparsiporous pollen and subringent corollas. It is not clear from Bremekamp's key in what genus our species would fall, although he stated that the closest allies of *Ruellia* L. emend. Bremek. are *Aphragmia* (based on *Ruellia inundata* HBK.) and *Arrhostoxylum* (based on *A. glabrum* Nees), both restricted to tropical and subtropical America. Most of our species possibly would fall into *Aphragmia*, resembling *Ruellia* in pollen, inflorescence, and seed characters, but differing in the clavate capsules with fewer seeds per capsule. Bremekamp also suggested that perhaps our species ought to be transferred to a new genus based on *R. strepens* L.

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Subtribe **Petalidiinae** Lindau emend. Bremek.

6. **Dyschoriste** C. G. D. Nees in Wallich, Pl. Asiat. Rar. **3:** 75, 81. 1832.

Perennial caulescent herbs [sometimes suffrutescent at base] with

glabrous or (more often) pubescent, erect, ascending [or prostrate] stems. Leaves sessile, subsessile [or petioled], usually entire [frequently fascicled]. Flowers in axillary clusters or cymes, sometimes solitary [rarely racemose], purplish, blue, or less commonly white, subtended by linear to oblong foliaceous bracts and bracteoles. Calyx deeply 5-cleft, lobes usually linear or subulate-setaceous, ciliate. Corolla-tube incurved or straight, cylindrical, often slightly ampliate at base, limb oblique, spreading, nearly regular to distinctly bilabiate. Stamens didynamous, a short and a long filament connate below and adnate to corolla tube, pubescent; anthers 2-loculate, more or less distinctly mucronate or aristate at base, locules equal, oblong, parallel to slightly divergent; pollen 3-colporate, prolate or occasionally subprolate, 40–50 × 47 × 28 μ. Stigma linear, anterior lobe somewhat flattened, oblique, posterior lobe rudimentary or absent; style filiform; ovary 2-locular, glabrous, ovules 2 or occasionally 1 in each locule. Capsule included in the persistent calyx, oblong-linear, 2–4-seeded, glabrous, separating with difficulty at maturity into 2 valves with 1 or 2 seeds within each valve held in position by the retinacula; capsule base contracted into a solid stipe; septum adnate. Seeds flat, orbicular or suborbicular, mucilaginous when wetted, hairs with faint rings or spiral thickenings within. (Including *Calophanes* D. Don, *Apassalus* Kobuski.) LECTOTYPE SPECIES: *D. depressa* (Wall.) Nees; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 240. 1913. (Name from Greek *dys*, difficult, and *choristos*, separable, in reference to the tenaciously coherent valves of the capsule.)

About 100 species widely distributed in the tropics and subtropics, with a few taxa extending into the warm-temperate regions of the world. About 40 supposed species are American, but it is probable that a monographic revision will reduce this number substantially.

Two species and two varieties occur in our area. *Dyschoriste humistrata* (Michx.) Kuntze (*Apassalus humistratus* (Michx.) Kobuski) is locally abundant in rich, sandy loam, limestone materials, and low river terraces from north-central Georgia to central peninsular Florida. *D. oblongifolia* (Michx.) Kuntze var. *oblongifolia*, $2n = 30$, is found on the Coastal Plain from South Carolina to Sarasota and Brevard counties, Florida, westward to Louisiana, in disturbed areas, sandy soil, pine barrens, and sandhills. It is quite variable both in leaf size and in pubescence of the stems and sepals. An endemic variety, *D. oblongifolia* var. *angusta* (Gray) R. W. Long,[6] is locally abundant in extreme southern Florida and the Florida Keys in moist pinelands, disturbed sites, especially burned-over areas, rocky roadsides, limestone rocks, and similar places.

Nees (1832) established the genus by the transfer of species of earlier authors from *Ruellia* and *Justicia*. The key characters used were ". . . antherae bilocellatae, locellis parallelis aequalibus basi mucronatis. Capsula . . . prope a basi tetrasperma. . . . Dissepimentum adnatum." Only

[6] **Dyschoriste oblongifolia** var. **angusta** (A. Gray) R. W. Long, comb. nov.
Calophanes angusta Gray, Synop. Fl. N. Am. 2: 324. 1878.
Dyschoriste angusta (Gray) Small, Fl. Miami 168. 1913; Fl. Florida Keys 135. 1913.

a year later David Don described his genus *Calophanes*, based on *Ruellia oblongifolia* Michx., apparently collected in Georgia. Both genera were used in later botanical literature, *Dyschoriste* representing Old World and *Calophanes*, New World taxa. Nees accepted this arrangement, but Bentham & Hooker, and later Clarke, placed *Dyschoriste* in the synonymy of *Calophanes*. Kuntze revived the earlier name; he was followed by Lindau, who placed the genus in his tribe Strobilantheae.

The complex problems in the typification of *Dyschoriste* have been discussed by Kobuski, who monographed the American species. His choice

FIG. 4. **Dyschoriste.** a–g, *D. oblongifolia* var. *oblongifolia*: a, flowering stem, × ½; b, node with two flowers, one bractlet removed from pedicel of flower at left, × 2; c, flower in longitudinal section, × 3; d, anther after shedding of pollen, × 8; e, stigma, × 10; f, ovary in vertical section to show placentation, diagrammatic, × 10; g, empty capsule with calyx removed — note retinacula, × 3. h–k, *D. oblongifolia* var. *angusta*: h, branch with fruit, × 1; i, empty capsule, × 3; j, seed with hygroscopic hairs, after moistening, × 12; k, embryo from moistened seed, × 12.

of *Ruellia erecta* Burm. as the type is based on Kuntze's transfer of *Ruellia erecta* to *Dyschoriste* thereby making it the oldest known epithet in the genus. The choice presumes the accuracy of the identity and synonymy of the several taxa, including *D. depressa* Nees, that Clarke referred to *Calophanes Nagchana* Nees. *Ruellia erecta* is typified by a reference of Burmann to a plate and description by Van Rheede. Unfortunately, the plant illustrated and described has alternate, lance-ovate leaves, annual roots, and an apparently one-lipped corolla. The calyx is described as four-parted, with two segments larger than the others. It is apparently not acanthaceous, but its true identity is uncertain. For the present the lectotype chosen by Britton & Brown seems to be the best available until the Old World plants can be examined.

Bremekamp (1955) transferred *Dyschoriste* from Strobilantheae to his Petalidiinae, a subtribe characterized by axillary cymes that rarely combine in a terminal panicle, by a subactinomorphic corolla never provided with a row of hairs functional in retaining the style, and, most importantly, by pollen grains that are prolate and banded, with three of the bands in the equatorial plane, dilated, and containing a pore. Most of the genera of the subtribe are tropical African in distribution, but *Dyschoriste* is pantropical. Kobuski decided not to place the American species in subgenera or sections because of the relative uniformity of morphological characters in the genus. Instead, he identified three distinct geographical areas where the species appear to be related: the southeastern United States (2 taxa); Texas and southern Arizona to the Isthmus of Tehuantepec (21 taxa); and South America (17 taxa).

Kobuski segregated his West Indian genus *Apassalus* from *Dyschoriste* on the basis of the much smaller leaves, smaller flowers, fruit characters, and muticous anther appendages. He considered it intermediate between the hypothetical ancestors of *Apassalus* and *Dyschoriste* proper in his interpretation. *Apassalus* was described as having only two seeds per capsule, but only one species (of three) has two seeds. The absence of anther appendages appears to be the only consistent character for the genus, and this hardly warrants recognition of a new genus in the Acanthaceae.

The phylogeny and relationships of *Dyschoriste* are obscure. The large number of closely allied species was considered by Kobuski probably to have evolved from common ancestral stock. He proposed that the taxa of the southeastern United States possibly are off-shoots of the widespread and morphologically generalized complex of *D. decumbens* (Gray) Kuntze, of Texas, Arizona, and Mexico, that developed parallel to the Mexican *D. Greenmanii* Kob. and *D. jaliscensis* Kob. Another morphological relationship is with the largely Texan *D. linearis* (Torr. & Gray) Kuntze. On the other hand, Kobuski thought that our southeastern taxa possibly are most closely related to his "*Apassalus* group" in the West Indies and have migrated into the United States from that direction. This theory assumes evolution of plants with large leaves, large flowers, anthers with appendages, and four-seeded capsules from plants with small flowers, muticous

anthers, and two-seeded capsules, a proposition that is difficult to accept. The absence of *Dyschoriste* in the Mississippi Valley does not rule out the possibility that the range of the genus prior to the Oligocene extended continuously across the southern United States. Possibly the distribution was then split into two parts by the encroachment of inland seas during later epochs of the Cenozoic. Such an interpretation would explain, at least in part, the relationship of our species with those of Texas and Mexico.

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Subtribe **Hygrophilinae** (Nees) Bremek.

7. **Hygrophila** R. Brown, Prodr. Fl. Nov. Holland. 479. 1810.

Perennial [or annual] erect, ascending [or diffuse] caulescent herbs; stems glabrous, sparsely pilose [or villous], unarmed [or with axillary spines]. Leaves entire, lanceolate to obovate. Flowers borne in axillary fascicles [or terminal heads, rarely solitary]; bracts linear [elliptic or lanceolate], ciliate; bracteoles lanceolate [or oblong], shorter than the calyx. Calyx tubular, segments 5 [4], equal to subequal, more or less fused to above the middle. Corolla tube cylindrical, ventricose at the apex, slightly ampliate; limb bilabiate, posterior lobe erect, concave, 2-cleft or 2-toothed, anterior segment 3-lobed, white [or pale purple]. Stamens didynamous [or 2 fertile stamens and 2 staminodia], not exserted, adnate to the tube above the middle; filaments glabrous, each pair connate at the base by a membrane, barely dilated; anthers oblong, muticous or submucronulate, 2-loculate, anther sacs parallel, divergent-sagittate. Pollen grains 3(4)-colporate, prolate spheroidal to subprolate spheroidal, varying in size from 35 × 33 μ to 70 × 66 μ. Disc inconspicuous. Style long, pubescent; stigma subulate, incurved, posterior lobe abortive; ovules usually 6–8 in each locule [or rarely 2, up to 18]. Capsule narrow, oblong,

nonstipitate, the partition adnate. Seeds 12–18 [rarely 4, up to 36], orbicular-compressed; retinacula short, obtuse, acute. TYPE SPECIES: *Ruellia ringens* L. = *H. salicifolia* (Vahl) Nees (*H. angustifolia* R. Br.); cf. T. Anderson, Jour. Linn. Soc. Bot. 7: 113. 1864. (Name from Greek *hygros*, wet, and *philos*, loving, a reference to the usual habitat of the plants.)

A pantropical genus of about 80 species primarily of the Old World tropics but with a number of species in tropical America. Nees's treatment (1847) is the only account of the entire genus. He informally divided the 24 species into two groups based on the morphology of the inflorescence. Bentham and Hooker interpreted the genus broadly, reduced a number of Nees's segregate genera to synonymy, and did not recognize any subgeneric categories. Clarke divided *Hygrophila* into two subgenera, HYGROPHILA (§ *Euhygrophila* Clarke) and ASTERACANTHA (Nees) Clarke, based on the presence or absence of spines, on calyx morphology, and on the number of seeds per capsule. He stated that *Hygrophila* may have 40–100 minute seeds per capsule (surely a mistake!) but cited no species with more than 32. Lindau (1895) recognized five sections, but *Asteracantha* Nees was treated as a separate genus. Our single representative belongs to the largest and taxonomically most difficult section, HYGROPHILA (§ *Euhygrophila* Clarke emend. Lindau), which is distributed from tropical Asia to tropical America.

Hygrophila lacustris (Schlecht.) Nees, $2n = 32$, occurs from southwestern Georgia and western Florida to eastern Texas, with its greatest development apparently in the lower Mississippi River valley and delta region. It is also found in the West Indies. The plant is a weak-stemmed perennial herb with narrow, sessile leaves and sessile axillary clusters of small white flowers. *Hygrophila lacustris* appears to be related to the widespread tropical *H. conferta* Nees, of Mexico and Central America. Nees observed that *H. lacustris* differs from *H. conferta* only in having sessile, attenuate leaves and somewhat smaller corollas. Other relationships, also in tropical America, may include *H. portoricensis* Nees and *H. brasiliensis* (Spreng.) Lindau. *Hygrophila polysperma* (Roxb.) T. Anders., a native of the East Indies, has been reported by Reams as quickly establishing itself in lakes at Richmond, Virginia, when introduced, but it is doubtfully naturalized.

Although *Hygrophila* is pantropical, its relationships are apparently with Old World genera, particularly with the African *Brillantaisia* Beauv. and the largely East Indian *Synnema* Benth. Lindau suggested intergeneric relationships also with the African genera *Eremomastax* Lindau and *Mellera* S. Moore, but Bremekamp believed these genera properly belong in the subtribe Petalidiinae. The Hygrophilinae resemble the Petalidiinae in inflorescence characters, but differ in the bilabiate corolla and distinctive pollen sculpturing. Typically, *Hygrophila* produces pollen with three, rarely four, germ pores that have four grooves between two of the pores.

Reams, in an examination of environmentally induced variations in the

morphology and ontogeny of two types of hydathodes (water stomata and water-secretory trichomes), found that submerged leaves have water-stomata but nonfunctional, recessed trichome-hydathodes, while aërial or emersed leaves produce functional, bulbous trichome-hydathodes and water-stomata. Hydathodes are replaced by simple hairs on the bracts. The differentiation of the three kinds of trichomes begins immediately after the second cell-division of the primordium. Other evidences of the essentially aquatic nature of this genus were noted by Solereder who described the typical lacunar, hydrophytic cortex and the peculiar appearance of the interlocking parenchyma cells around the air chambers.

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Tribe JUSTICIEAE Nees emend. Bremek.

Subtribe **Odontonematinae** Lindau emend. Bremek.

8. **Asystasia** Blume, Bijdr. Fl. Nederl. Indië 796. 1825 [1826].

Perennial herbs [or shrubs], [erect,] procumbent or clambering, pubescent [or glabrous]. Leaves [narrowly lanceolate or] ovate, entire or somewhat dentate. Inflorescences terminal simple or branched racemes [or spikes], often unilateral; flowers opposite or alternate, solitary or glomerate in axils or bracts; bracts linear to narrowly deltoid, bracteoles minute. Calyx lobes 5, linear-setaceous [or lanceolate], subequal. Corolla purplish, blue, yellow, or white, infundibuliform, the limb 5-lobed, the tube straight or incurved, long, narrow or ventricose, the throat ampliate

or campanulate; aestivation imbricate. Stamens didynamous, or occasionally the posterior pair reduced to filiform staminodia, included; anthers 2-loculate, muticous at base or mucronate, locules parallel, equal, approximate, or unequal; pollen 3-porate (pleurotreme), prolate. Disc cupulate or annular. Style subulate; stigma obtuse or minutely 2-parted (or subcapitate); ovary with 2 ovules per locule. Capsule stipitate, pubescent [or glabrous], elliptic, the base contracted and solid, adnate; seeds 2–4 or fewer by abortion. Seeds ovate or compressed orbicular, irregularly angular, rugose or tuberculate, glabrous, retinacula elongate, subulate. TYPE SPECIES: *A. intrusa* (Forssk.) Blume. (Name possibly from Greek *asystatos*, not holding together, in reference to the wide-spreading valves of the dehisced capsules.)

A genus of possibly 40 species (although about 70 have been described) native to the Old World tropics, chiefly in the East Indies, India, and Africa, and now thoroughly naturalized in the New World tropics.

Asytasia is represented in our flora by *A. gangetica* (L.) T. Anders. (*A. coromandeliana* Nees), $2n = 50, 52$, a native of India. The plant is apparently a rather recent introduction into southern Florida where it has become naturalized as a lawn weed and has been found growing along the margins of pinelands (*Lakela 28452*, GH, USF). Our specimens appear to be identical or closely similar to those from the West Indies and other areas of tropical America where the species is used as a ground cover and has escaped from cultivation. The corolla color varies from pale bluish lavender to yellow or white with purplish darker lines on the limb.

The genus is in critical need of monographic revision. Nees described 15 species in his treatment of *Asystasia* for DeCandolle's *Prodromus*, and he included 7 varieties in the most variable species, *A. gangetica*. Bentham & Hooker enlarged the genus to include two groups of shrubs, *Dicentranthera* T. Anders., from the African tropics, and *Mackaya* Harv., from South Africa. Lindau (1895) placed *Asystasia* in its own tribe, Asystasieae, on the basis of its distinctive pollen and reduced number of seeds per capsule, but Bremekamp, in his realignment of the Justicieae (1965), transferred the genus to his emended Odontonematinae.

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Subtribe **Justiciinae** Bremek.

9. **Dicliptera** Jussieu, Ann. Mus. Hist. Nat. Paris **9**: 267. 1807, nom. cons.

Perennial herbs [or shrubs], erect, ascending, or diffuse, pilose, hirtellous [or variously pubescent], with branching, often lax stems more or less hexagonal in cross-section. Leaves petioled, blades lanceolate to ovate, entire (or undulate). Flowers sessile, solitary or clustered in contracted cymes, these forming erect, secund, often lax spikes or panicles; bracts 2, frequently small, subulate; bracteoles 2 or 4, opposite in pairs and forming an involucel, the outer subequal, appressed, lanceolate or ovate. Calyx deeply 5-parted, the lobes linear-setaceous, equal or subequal, hyaline. Corolla red, violet, blue, pink, or white; tube narrow, resupinate, slightly ampliate; limb nearly regular or more often bilabiate, the upper lip entire, emarginate, or 2-toothed, flat or concave, the lower lip spreading, slightly 3-lobed; aestivation imbricate. Stamens 2, exserted but shorter than the upper lip, staminodia absent; anthers 2-loculate, anther sacs often unequal, muticous or the longer ones sometimes spurred; pollen 3-colporate, prolate or rarely perprolate, mostly 60×25 μ in diameter. Disc cupular, oblique-truncate, or sinuate-dentate. Style filiform; stigma entire or minutely 2-toothed; ovary with 2 ovules per locule. Capsule ovoid to suborbicular, subsessile, contracted into a short, solid stipe; placentae separating elastically from the walls and rupturing on dehiscence. Seeds 4 [or 2] or fewer by abortion, lenticular, with smooth, muricate, or squamose surface; retinacula uncinate, broadened at the base, acute tipped. (Including *Diapedium* Konig, nom. rejic., *Yeatsia* Small, *Gatesia* Gray.) TYPE SPECIES: *D. chinensis* (L.) Juss., typ. cons. (Name from Greek *diklis*, folding two ways, a double or folding door (*i.e.*, having two valves), and *pteron*, wing, in reference to the two recurved, apparently winged valves of the dehisced capsule.)

A large, taxonomically complex genus of possibly 150 species (although according to Leonard nearly 300 have been described) in the tropics, subtropics, and warm-temperate regions of the world, best developed in the East Indies, South Africa, and tropical South America. Three species in three sections occur in our area.

Section DICLIPTERA (§ *Platystegiae* Nees) is characterized by orbicular, ovate or elongate-ovate bracteoles, the bases not cuneate. *Dicliptera viridiflora* (Nees) R. W. Long,[7] an endemic species of southwestern

[7] **Dicliptera viridiflora** (Nees) R. W. Long, comb. nov.
Rhytiglossa viridiflora Nees in DC. Prodr. **11**: 346. 1847.

Georgia and adjacent Florida in rich, wooded bottomlands of the Flint and Apalachicola rivers, where it may be locally abundant, has white, pale blue, or pink, nearly regular corollas in compacted spikes with conspicuous, ovate, acuminate bracts. The species appears to be morphologically close to the West Indian *D. martinicensis* Juss.

Section SPHENOSTEGIAE Nees, the largest subgeneric group, is characterized by floral bracts more or less cuneate at the base and is represented with us by *D. brachiata* (Pursh) Spreng. var. *brachiata* (*Diapedium brachiatum* (Pursh) Kuntze, *Diapedium attenuatum* (Gray) Heller), $2n$ = ca. 80. Recognizable by its green, rather broad, wedge-shaped bracts, usually large, ovate-lanceolate to elliptic, long-petioled leaves, and strongly bilabiate, pink or reddish corollas, this erect herb is widely distributed on the Coastal Plain from Virginia to Texas, inland to Arkansas, Missouri, and Kansas in river bottoms, hammocks, and low ground. It is variable in morphology of leaf, bract, and pubescence; differences in the latter caused Fernald to describe two minor varieties from Texas.

Section DACTYLOSTEGIAE Nees is a small group of tropical American species characterized by the presence of two floral bracts larger than others in the involucel. Our representative is *D. assurgens* (L.) Juss. (*Diapedium assurgens* (L.) Kuntze), $2n$ = 80, a West Indian weedy species characterized by stiffly erect stems, and conspicuous bright red or scarlet bilabiate corollas in narrow, terminal or axillary lax panicled spikes. Two varieties, both occurring in peninsular Florida, have been distinguished. Varietas *Vahliana* (Nees) Gomez (*D. Vahliana* Nees), with spatulate-mucronate outer involucel bracts, occurring from Lake County, south into the Florida Keys, is often common along roadsides, on shell mounds, in coral soil, and in hammocks. Less frequently, var. *assurgens*, characterized by subulate-attenuate bracts, can be found in extreme southern Florida, from Sanibel Island, Lee County, to the Florida Keys.

There is some evidence that polyploidy has been an important cause of variation in *Dicliptera*. Grant pointed out that both *D. assurgens* and *D. brachiata* are tetraploids in comparison with the Central American *D. resupinata*, which Sigiura reported as having a gametic chromosome number of 20. Because of their morphological similarities, it is possible that *D. brachiata* may have been derived either as an autopolyploid or allopolyploid derivative of *D. resupinata*. Kaur has reported the chromosome number of *D. elegans* as $2n$ = 20 and that of *D. Leonotis* as $2n$ = 48. Additional chromosome counts for *Dicliptera* species are very desirable.

In the only treatment for the entire genus, Nees (1847) established five sections (based on the morphology of the floral bracts), which were accepted, in general, by Lindau (1895). Initially, Bremekamp (1943) accepted Lindau's placement of *Dicliptera* in the tribe Odontonemateae,

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Dicliptera Halei Riddell, New Orleans Med. Surg. Jour. **8**: 756. 1852.
Gatesia laete-virens Gray, Proc. Am. Acad. Arts Sci. **13**: 365. 1878.
Justicia laetevirens Buckley, Am. Jour. Sci. **45**: 176. 1843, not *J. laetevirens* Vahl.
Yeatsia laete-virens (Buckl.) Small, Bull. Torrey Bot. Club **23**: 405–410. 1896.

subtribe Diclipterinae but later transferred the genus to his emended Justicieae. Intergeneric relationships appear to be closest with the Old World tropical genera *Hypoëstes* Soland. ex R. Br. and *Peristrophe* Nees, and possibly with *Rungia* Nees (although Bremekamp suggested that pollen and capsule characters indicate that *Rungia* ought to be in a different subtribe from *Dicliptera*). Pollen sculpturing apparently is not as useful a taxonomic tool in the Justicieae as in some other tribes of Acanthaceae. Eight different pollen types have been reported from a single anther of *D. javanica* (cf. Davis)!

Dicliptera needs a critical taxonomic review because the proposed intergeneric relationships and intrageneric alignments appear to be highly artificial, if not simply arbitrary. The present construction of subgeneric categories based on minor differences in the morphology of floral bracteoles does not seem to reflect any natural relationships of species groups within the genus. This emphasis on small differences has carried over into the description of species. Leonard included 29 species, 26 of them new, in his account of *Dicliptera* in Colombia. Morphological criteria for the separation of many of these new species are minimal, and it is probable that future study will prove them unworthy of taxonomic recognition.

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10. **Justicia** Linnaeus, Sp. Pl. 1: 15. 1753; Gen. Pl. ed. 5. 10. 1754.

Perennial herbs [rarely shrubs] with erect or ascending, smooth or variously pubescent stems. Leaves petiolate, linear, lanceolate, or more often ovate to oblong, entire. Flowers small or moderately large, fascicled, or in lax terminal or axillary cymes, spikes or panicles [or solitary]; bracts various, often small, linear or subulate, distant, or sometimes both bracts and bracteoles conspicuous, large, imbricate. Calyx deeply 5 [or sometimes 4]-parted, cleft nearly to the base, segments subulate or linear, acute, nearly equal. Corolla white, red, pink, purple, sometimes with purple or white markings in the throat; tube short [rarely long], straight

or incurved, rather narrow, slightly ampliate above; limb bilabiate the upper lip erect or concave, incurved, spreading, frequently 2-dentate, external in bud, lower lip 3-lobed. Stamens 2, staminodia none, usually slightly exserted but not exceeding the corolla lips, adnate to the throat of the corolla; anther 2-loculate, anther sacs separated, more or less superposed, one or both sacs apiculate or produced into a spur or tail, lobes parallel or obliquely affixed, connective broad or narrow; pollen grains 2-porate, bilateral, ca. 66 × 47 × 40 μ, 3-colporate (pleurotreme), subprolate, ca. 28 × 22 μ. Disc cupulate or cyathiform, entire or sinuately 2- or 3- or 5-lobed. Stigma entire, capitate, or minutely 2-dentate; style filiform; ovules 2 in each locule. Capsule ovate, oblong, clavate [or orbicular], contracted at the base into a short, solid stalk. Seeds 4 [or 2] or fewer by abortion, plano-compressed, suborbicular, smooth, foveolate-rugose, tuberculate or muricate; retinacula arcuate, acute, truncate below. (Including *Dianthera* L., *Beloperone* Nees, *Rhytiglossa* Nees, *Drejerella* Lindau.) LECTOTYPE SPECIES: *J. hyssopifolia* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 116. 1929. (Named in honor of James Justice, a Scottish botanist and horticulturist of the 18th century, author of *The British Gardener's Calendar*, 1754.) — WATER-WILLOW.

The largest genus in the family with about 300 species distributed throughout the tropics and subtropics of both hemispheres and extending into the temperate region of North America.

The most widespread *Justicia* of our area is *J. americana* (L.) Vahl (*Dianthera americana* L.; including *J. mortuifluminis* Fern.), $2n = 26$, the common water-willow of margins of ponds, lakes, rivers, and occasionally swamps throughout most of the eastern United States and probably even into Mexico. *Justicia ovata* (Walt.) Lindau var. *ovata* (*J. humilis* Michx.) occurs on the Coastal Plain in swampy woods, shallow water, and bottomlands from southern Virginia to northern Florida; var. *lanceolata* (Chapm.) R. W. Long,[8] $2n = 14, 14 + 1$, is found in wet soil and bottomlands from central Florida and Tennessee, west to Louisiana and Texas; var. *angusta* (Chapm.) R. W. Long,[9] a narrower-leaved, smaller-flowered plant occurs as an endemic in central Florida, also in marshy places. Two other well-marked, endemic species also occur in Florida: *J. crassifolia* (Chapm.) Small is found in wet pinelands and glades in Gulf County at the mouth of the Apalachicola River, and *J. Cooleyi* Leonard & Monachino has been found in hammocks on limestones in Her-

[8] **Justicia ovata** (Walt.) Lindau var. **lanceolata** (Chapm.) R. W. Long, comb. nov.
Dianthera ovata var. *lanceolata* Chapman, Fl. So. U.S. 304. 1860.
J. lanceolata (Chapm.) Small, Man. Southeast. Fl. 1231. 1933.
J. humilis Michx. var. *lanceolata* (Chapm.) Gleason, Phytologia **4**: 24. 1952.

[9] **Justicia ovata** (Walt.) Lindau var. **angusta** (Chapm.) R. W. Long, comb. nov.
Dianthera ovata var. *angusta* Chapman, Fl. So. U.S. 304. 1860.
J. angusta (Chapm.) Small, Man. Southeast. Fl. 1231. 1933.

nando County. A Mexican species, *J. Brandegeana* Wasshausen & Smith [10] (*Beloperone guttata* T. S. Brandeg., *Drejerella guttata* (T. S. Brandeg.) Bremek.), has escaped and apparently become naturalized in peninsular Florida, especially in waste places, citrus groves, and around former habitations. This is the common "shrimp plant" that is grown widely for its attractive spikes of reddish-brown or greenish-yellow, ovate bracts and white flowers.

Our species need careful revision, for it is apparent that some of the forms intergrade and may, therefore, be conspecific. Experimental hybridizations should be especially useful in determining interspecific relationships, particularly in the *J. ovata* complex. It appears that our species are not closely related to tropical American taxa, although possibly *J. americana* may be allied to certain Mexican and Central American groups. *Justicia ovata* and *J. crassifolia* are possibly related to West Indian and Central American taxa, such as *J. secunda* Vahl and *J. filibracteolata* Lindau. Monachino and Leonard thought that *J. Cooleyi* is related to *J. Pringlei* Robins., of Mexico, and to *J. galapagana* Lindau, of the Galapagos Islands.

The taxonomic history is so complex that only a general review, and that only with special reference to taxa of our area, is possible here. Nees described the North American species under his *Rhytiglossa*, a confused assemblage of dissimilar elements supposedly from South Africa and America. He placed the genus in his tribe Aphelandreae, but later Bentham & Hooker transferred the group to their Justicieae and included it under *Dianthera*. For the most part, Bentham & Hooker followed Anderson in his general circumscription of *Justicia*, although he also included *Adhatoda* Medic. Bentham & Hooker recognized 11 sections in *Justicia*, but *Beloperone* and *Dianthera* were considered to be separate genera. It is not altogether clear from their descriptions where our species would be placed, but presumably they would be under *Dianthera*.

Lindau (1895) divided *Justicia* into three subgenera, JUSTICIA (subg. *Eujusticia* Lindau), GENDARUSSA (Nees) Lindau, and DIANTHERA (L.) Lindau based on morphology of the inflorescence and anther sac and to some extent on pollen sculpturing. Subgen. JUSTICIA, the largest division, was further divided into seven sections, three of which contained American taxa. Our species all belong to subgen. DIANTHERA which supposedly is characterized by blunt or short-stalked anther sacs.

Bremekamp (1948) was of the opinion that the generic circumscriptions of Anderson, Bentham, and Lindau were too vague and that their definitions of *Justicia* could not be held together any longer. He recommended that *Justicia* be confined to *J. hyssopifolia* L., of the Old World, and

[10] **Justicia Brandegeana** Wasshausen & L. B. Smith, Fl. Illus. Catarinense 1(Acan): 102. 1969.

Beloperone guttata T. S. Brandegee, Univ. Calif. Publ. Bot. **4**: 278. 1912; non *Justicia guttata* Wall. Pl. Asiat. Rar. **1**: 24. *pl. 28*. 1830.

Calliaspidia guttata (T. S. Brandeg.) Bremek. Verh. Nederl. Akad. Wet. Afd. Natuurk. 2. **45**(2): 54. 1948.

Drejerella guttata (T. S. Brandeg.) Bremek. Philip. Jour. Sci. **80**: 14. 1952.

FIG. 5. **Justicia.** a–g, *J. ovata* var. *angusta*: a, small plant with flower, × ½; b, flower and flower buds, × 3; c, anther, × 10; d, disc and ovary with one side removed to show four ovules, × 12; e, drying fruit, one seed removed — note retinacula, × 3; f, moistened seed, × 6; g, embryo from same, × 6. h, *J. crassifolia*: opening fruit with two seeds, four retinacula, × 3. i–l, *J. Cooleyi*: i, flower and bud, lateral view, × 4; j, corolla with one stamen, opened out, × 4; k, anther, from below, × 10; l, partially mature fruit and flower from which corolla has fallen, × 2. m, n, *J. americana*: m, corolla with stamens, from above, × 3; n, anther from below, × 10.

Dianthera (based on *D. americana* L.) be restricted to the New World. There is no evidence from pollen morphology to suggest that *Dianthera* ought to be retained as a genus, although Grant thought there is some cytological basis for recognizing the genus. The slight morphological difference for their separation is based on the position of the anther sacs, which are stalked obliquely at the tip of a branched connective in *Dianthera*, while in *Justicia* one anther sac is borne horizontally or obliquely at the tip of the connective and one is borne perpendicularly, or nearly so, below it. In both instances the anther sacs are blunt, not pointed at the base, a character Lindau considered of sufficient weight to place all species of *Justicia* of the United States in his subgen. DIANTHERA. Leonard (1958) united both *Dianthera* and *Beloperone* under *Justicia* after pointing out that continuous variation in anther characters made it impractical to maintain the separate genera. Bremekamp transferred *Beloperone guttata* to still another segregrate genus, *Drejerella*. Until additional evidence is available, a broad interpretation of the genus appears to be more in keeping with the facts.

Inter- and intrageneric relationships in *Justicia* have been the subject of a wide variety of investigations. Mohan Ram & Sehgal studied pollen-grain formation, embryo-sac development, and embryogeny in *J. simplex* D. Don, a native of tropical Africa and Asia. They reported that chalazal haustoria generally are two-nucleate in *Justicia*, as in *Beloperone* and *Adhatoda*. No significant embryological differences were found between the three genera. *Dicliptera* and the African genus *Barleria* also resemble *Justicia* in the morphology of the chalazal haustoria, but *Blechum*, *Ruellia*, and *Hemigraphis* produce four-nucleate haustoria. The broad basal apparatus characteristic of the three latter genera is represented by a rudimentary, few-nucleate structure in *Justicia*.

Palynological and cytological investigations of taxonomic relationships have generally been inconclusive. Raj was not able to find any differences between the pollen grains of *Justicia* and *Dianthera*. However, Bhaduri concluded that Lindau subordinated *Adhatoda* as a section in *Justicia* because he misconstrued the morphology of the pollen of *A. vasica* (*J. Adhatoda*) and further concluded that the two genera should be separate. Bentham & Hooker maintained *Adhatoda* as a separate genus on the basis of other morphological grounds, but Leonard (1958), apparently on similar bases, submerged *Adhatoda* in *Justicia*. Grant concluded there is sufficient evidence to retain *Adhatoda* as a separate genus because the somatic chromosome number typically is $2n = 54$. *Justicia* species are known with $2n = 28$, 32, and 36, suggesting three basic numbers: $x = 7$, 8, and 6 or 9. The same numbers are also found in *Beloperone* and *Jacobinia*. Grant suggested that aneuploidy is a probable cause for the diversity in chromosome number in *Justicia* and that possibly related groups, such as *Adhatoda*, arose through allopolyploidy. The discovery of "B" chromosomes in *J. ovata* var. *lanceolata* (cf. Lewis *et al.*) may be evidence of the occurrence of aneuploidy that perhaps was caused by fragmentation of chromosomes or is a vestige of reduction from higher ploidy levels. Additional

cytological studies should be useful in any future intrageneric studies, but crossing experiments might be more helpful at this point.

Unlike many *Ruellia* species, *Justicia* populations may be largely if not entirely allogamous. Although no hybridization studies have been made, there is some evidence that outbreeding occurs regularly in *J. simplex*. Jain & Joshi conducted a genetic analysis of gene frequencies at a petal-color locus in local populations and concluded that the tendency for markedly local differentiation in these polymorphic plants could best be explained by considering them as partially isolated, panmictic populations. Additional investigations of causes of variation in the genus ought to include artificial hybridization experiments to ascertain whether barriers to crossing occur between species. It is possible that some of the observed patterns of variation in our species are caused by natural hybridization.

Future work on *Justicia* may result in additional evidence that would provide a basis for splitting up the genus into two, three, or more segregate genera. At the present time the evidence for this course of action is equivocal, but it seems clear that most of our southeastern species are more closely related to one another than they are to other taxa outside of the range of the Flora. If segregate genera are to be recognized they would be *Dianthera* L. (based on *D. americana* L.), *Adhatoda* Nees (based on *Justicia Adhatoda* L. = *A. vasica* Nees), and *Justicia* (based on *J. hyssopifolia* L.).

Justicia species have also been used in various other biological and chemical investigations. Anatomical and morphological studies have been reported by Sterling, Jones, *et al.*; studies of toxins, alkaloids, and other chemical constituents have been carried on by Munakata *et al.* and Bhatnagar & Popli; and pollination studies by Buxbaum. Many of the attractive cultivated plants that pass under the name *Justicia* properly belong to the tropical American genus *Jacobinia* Nees ex Moric.

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FLORAL MORPHOLOGY AND VASCULAR ANATOMY OF THE HAMAMELIDACEAE: THE APETALOUS GENERA OF HAMAMELIDOIDEAE

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THE HAMAMELIDACEAE ARE A FAMILY of twenty-seven genera and possibly 100 species distributed in the tropical, subtropical, and temperate regions of both the New World and the Old. The genera are small, fourteen are monotypic, six contain only two to three species, while seven comprise from five to fourteen species. Most of the genera are narrow endemics or very restricted in their distribution, only two (*Hamamelis*, *Liquidambar*) being present in both Asia and North America. The genera are morphologically diverse, ranging from huge evergreen trees to low deciduous, rhizomatous shrubs. Their leaves vary from palmately lobed and veined to elliptic-oblong and pinnately veined and may be spirally arranged, two-ranked, or opposite. They are stipulate in all genera except one (*Rhodoleia*). Inflorescences vary from simple racemes to panicles, spikes, heads, or densely congested and fused, complex, capitate flowering branch-systems. The flowers may be showy or inconspicuous, petaliferous, apetalous or naked, bisexual or unisexual, with few to numerous stamens, many ovules to only one, and few winged seeds per carpel to mostly a single wingless seed. Perhaps the one unifying morphological feature of the family is in its characteristic 2(–3)-carpelled, septicidal (and sometimes partially loculicidal as well) woody, capsular fruits.

The morphological, systematic, and phyletic relationships of the Hamamelidaceae were last reviewed in detail forty years ago (Harms 1930). Many of the problems encountered then concerning morphological interpretations and systematic or phylogenetic affinities have remained unresolved up to the present time. Furthermore, in the intervening years, the concept of the family has been expanded through the discovery or recognition of new genera which have increased its diversity, rather than bridged its internal gaps. Indeed, the diversity of the family is such that some consider two or more families to be represented, rather than one. The limits of some tribes, or the tribal affinities of a few genera are uncertain, while the morphological nature of certain floral organs has evaded satisfactory interpretation in some cases, or has been widely misinterpreted in others. These problems have prompted several workers, in recent years, to point out the need for more detailed study of the group. Foremost among the areas in need of examination is that of floral vascular anatomy, which has only recently come under scrutiny (Bogle 1967, 1968, 1969; Endress 1967; Horne 1914). Evidence from such studies in other groups has been very valuable in the interpretation of difficult problems of floral morphology, which is among the principal bases on which systematic and phylogenetic relationships may be established.

This paper is the first in a series which will provide a detailed comparative account of the floral vascular anatomy, coupled with other observations on floral and inflorescence morphology, for each of the 27 known genera of the family. The ultimate purpose of this work is the clarification of the morphological homologies of the organs of the hamamelidaceous "flower," and of the phylogenetic trends among the divergent floral types within the family. Such information, along with evidence from other lines of research, should then permit a re-evaluation of the interfamilial and phylogentic relationships of the Hamamelidaceae. The opinions expressed in the literature concerning this family differ widely. It has been thought to be 1), related to several extant magnolialian families, or directly derived from a magnolialian or proto-magnolialian stock (Solereder 1899; Hallier 1903, 1912; Tippo 1938; Tang 1943; Chang 1961; Cronquist 1968; Takhtajan 1969); or 2), derived from a rosalian or proto-rosalian stock, with close affinity to the extant Rosaceae, Saxifragaceae, or more especially the Cunoniaceae (Bentham & Hooker 1865; Baillon 1871, 1874; Eichler 1875; Reinsch 1889; Niedenzu 1891; Bessey 1915; Hutchinson 1926, 1959; Tong 1930; Harms 1930; Melchoir 1964; Endress 1967; Jay 1968); or 3), to be derived from an amentiferous ancestral stock (Wettstein 1935; Croizat 1960, 1964). On the other hand, many of the authors cited above derive from a proto-hamamelidalian stock the highly specialized and advanced group of families included in the "Amentiferae" (particularly the Betulaceae, cf. Endress 1967) which are characterized by greatly condensed inflorescences and reduced, typically unisexual, monochlamydeous, wind-pollinated flowers. The authors mentioned above who view the "Amentiferae" as primitive, however, consider the Hamamelidaceae and its allies transitional to the more advanced Polycarpicae, Rosales, or Cornales, with dichlamydeous, bisexual flowers, but this view receives little support from current workers.

MATERIALS AND METHODS

All of the specimens collected in the field in Southeast Asia and Mexico for anatomical study were preserved in fluid. Fresh specimens were preserved in formalin-acetic acid-alcohol (F.A.A.) for the most part, or in 70 per cent ethyl alcohol. With collections in Hong Kong, however, a reasonable preservation was achieved with a makeshift solution consisting of equal parts of Rectified Spirits of Wine B.P., and distilled white vingar, giving concentrations of about 50 per cent ethyl alcohol and 2.5 per cent acetic acid. These specimens were later transferred to F.A.A. Flowers from herbarium specimens have been used for a few genera, but were often found to be unsatisfactory for anatomical purposes due to distortion and rupturing of the tissues caused by pressing, drying, and re-expansion. Flowers at both anthesis and post-anthesis stage were sectioned when available, since the ovary and its vasculature are poorly developed in some genera at flowering time.

Cleared and uncleared whole flowers, hand sections, and serial microtome

sections were utilized according to the nature of the material to be examined. Flowers from herbarium specimens were softened and re-expanded, using the modified Juel method described by Tillson & Bamford (1938), and then treated as fresh material.

Specimens to be cleared were first soaked in water to remove excess F.A.A., then bleached to near-whiteness at room temperature in a solution consisting of nine parts 2.5 per cent sodium hydroxide to one part 5 per cent sodium hypochlorite or commercial Clorox. The bleaching solution was rinsed out thoroughly with water before gradual dehydration followed by clearing in xylene, chloral hydrate, or paraffin oil. Where necessary and possible, pubescence was removed from floral surfaces after clearing in xylene, when the brittle epidermis lifts off easily.

Flowers to be sectioned were of necessity bleached and softened. Untreated flowers proved generally unsatisfactory for sectioning and staining due to 1), tearing of the sections caused by the hardness of the lignified, often dense epidermal pubescence, or hard internal tissues such as the developing bony endocarp, or 2), the presence of densely staining organelles or intracellular substances of undetermined nature with a particular affinity for safranin, which often obscure the vasculature. A distinct disadvantage of this harsh process is the collapse of cells that it may cause in delicate parenchymatous epidermal surfaces, as in young ovules, or the transmitting tissues of the stylar canal, etc. After bleaching, the flowers were dehydrated in a normal-butyl or tertiary-butyl alcohol series, embedded in "Paraplast," and sectioned at 10, 15, or 20 micra, depending on the size of the flower.

Various stain combinations were tried, including erythrosin and crystal violet, safranin and anilin blue, safranin and fast green, and Foster's tannic acid-iron chloride (Johansen 1940). The last two methods gave the most satisfactory results for tracing vasculature, and were used almost exclusively. Polarized light was frequently used to aid in tracing small vascular bundles.

Drawings were made with the aid of the drawing attachments designed for the Wild M–20 and M–5 microscopes. The floral pubescence so obscures the outlines of the floral organs in many genera that it has been omitted in most of the figures for the sake of clarity.

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tion and study of critical Old World genera in Southeast Asia, and took an active interest in the progress and results of the work. It is impossible to thank my wife, Margaret, enough for her help during the course of this project.

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The curators of the following herbaria have allowed me to borrow specimens or to examine their collections; to all of them I express my appreciation: the Arnold Arboretum and the Gray Herbarium of Harvard University, the Chicago Natural History Museum; the University of Michigan Herbarium; the University of Minnesota Herbarium; the Herbarium of the Department of Botany of the United States National Museum; the Herbarium of the Urban Services Department, Hong Kong; the Herbario Nacional del Instituto de Biología, Universidad Nacional Autónoma de México; the Muséum National d'Histoire Naturelle, Paris; the Philippine National Herbarium, Manila; the Herbarium of the Botanic Gardens, Singapore; and the Herbarium of the Taiwan Forestry Research Institute.

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GENERAL CONSIDERATIONS

For the purposes of this work the genera of the family will be considered as comprising three fairly natural groups. The apetalous tribes and genera of the Hamamelidoideae (Distylieae: *Distylium*, *Sycopsis*, *Matudaea*, *Molinadendron;* Fothergilleae: *Parrotia*, *Parrotiopsis*, *Fothergilla*) will be

considered here, followed later by the petaliferous Hamamelidoideae (tribes Hamamelideae, Eustigmateae, Corylopsideae), and finally the four small and distinct tribes Liquidambaroideae, Rhodoleioideae, Disanthoideae, and Symingtonioideae. The order of consideration of the genera here differs somewhat from that given in the system of Harms (1930, as revised by Melchior, 1964, and with four tentatively placed genera included), which is the most comprehensive available.

The tribe Distylieae Hallier (1903) originally contained only *Distylium* Sieb. & Zucc. and *Sycopsis* Oliv. and was characterized by Hallier (op. cit., p. 255) as follows: Leaves leathery, entire or toothed, evergreen, with small lanceolate stipules, spicular cells, two-layered palisade tissues, and small single crystals. Inflorescences pedunculate, solitary, of axillary heads or racemes; bracts small; flowers monoecious or andromonoecious, lacking petals; anthers oblong, narrowed below to a short filament and above into a short point, dehiscing by two lateral, longitudinal, simple slits.

The Central American genus *Matudaea* Lundell (Lundell 1940) was considered by Walker (1944) to conform in most respects with Hallier's description of the tribe, and has been tentatively included in it. Walker also maintained two Central American species of *Distylium* which, with a third species since described, were recently and rightfully removed as the segregate genus *Molinadendron* Endress (Endress 1969). Endress considers *Molinadendron* misplaced in the Distylieae, and closer to *Fothergilla* and *Parrotiopsis* (*Fothergilleae*) or to *Fortunearia* and *Sinowilsonia* (Corylopsideae). The genus *Sinowilsonia* Hemsl. (Hemsley 1907) was added to the Distylieae (Harms 1930) but later removed to the Corylopsideae (Schulze-Menz 1964). I shall describe it with the petaliferous Hamamelidoideae.

Leaf venation in the Distylieae is pinnate. In *Molinadendron* the veins terminate in the distal, marginal teeth, but in the other three genera the veins are, for the most part, curved-anastomosing (camptodromous type) well within the margins, or in a few species basally triplinerved (*Matudaea*, *Sycopsis laurifolia*) and approaching a camptodromous condition.

The tribe Fothergilleae DC. (1830) contained only *Fothergilla* L. Niedenzu (1891), however, recognized a tribe Parrotieae which combined the apetalous genera *Distylium*, *Parrotia* C. A. Mey., and *Fothergilla* (including *Parrotiopsis*) with the petaliferous *Corylopsis* (*Sycopsis* was placed in the tribe Hamamelideae between *Eustigma* and *Hamamelis*). The tribe Fothergilleae in Harms's system (1930) contains *Fothergilla*, *Parrotia*, and *Parrotiopsis* (Niedenzu) Schneid., and is characterized in his key to the family (op. cit., p. 315) as having flowers perfect, in congested spikes or small heads. Petals lacking. Stigma punctiform or capitate. Number of floral parts irregular. Stamens often more than five. Anthers dehiscing by longitudinal slits or valves.

The leaves of the three genera of Fothergilleae are membranous, stipulate and deciduous, with ascending, often more or less parallel pinnate veins which terminate in the distal lobes of the sinuate-dentate to coarsely toothed margins (craspedodromous type).

The structure of the ovary is rather uniform within the Hamamelidoideae. Therefore, a general description is provided at this point in order to avoid repetition in the generic descriptions below. The trends of vascular specialization will be discussed later for the entire subfamily.

The gynoecium consists of two, or not infrequently three, involute carpels. The carpel margins are fused below, and the carpels united adaxially through the length of the ovary, forming an incompletely septate, essentially bilocular capsule. The two locules become confluent above, just below the level of ovule insertion near the apex of the locules, as the opposing fused adjacent carpel margins incorporated in the septum separate to form the parietal placentae. Above the ovules the ovarian cavity continues upward as a narrow, elongated canal which opens to the outside through the style bases. Above the ovary the carpels are free, in the Distylieae and Fothergilleae terminating in exserted, linear-subulate styles which are often recurved, and sometimes slightly expanded, bearing extensive exposed or included papillate stigmatic surfaces along their ventral faces. One or occasionally two, pendent, anatropous ovules may occur in each carpel, inserted on both margins, but usually only one of these (occasionally two) is functional.

Each carpel is supplied with five bundles: the dorsal midvein, two submarginal lateral bundles, and two marginal ventral bundles. In the syncarpous ovary the lateral bundles or adjacent fused carpel walls are incorporated in discrete or diffuse compound lateral bundles (the synlaterals of Endress, 1967; lateral bundles of Horne, 1914) which ascend at each edge of the septum. The compound laterals may dichotomize to form individual lateral bundles well below the level of ovule insertion, or remain united almost to the top of the ovary, where they fuse with the ventral bundles. With few exceptions the ventral bundles arise in the septum from a narrow, largely procambial remnant of the receptacular cylinder (the inner series of Horne, 1914), which enters the base of the septum before consolidating as a single axial bundle (the synventralmedian of Endress, 1967) and dividing to form two compound ventral bundles (the synventrals of Endress, the septal or placental bundles of Horne). The ascending compound ventrals may also divide to form distinct ventral bundles well below the level of ovule insertion, or remain united to the level of fusion with the lateral bundles near the top of the ovary. After fusing with the lateral bundles the ventrals continue upward into the margins of the style. Each functional ovule receives a single trace from the adjacent ventral or compound ventral bundle. No traces have been observed to supply abortive ovules. Within the ovary walls the dorsal and lateral bundles supply lateral branches to the vascular network of the carpels. At anthesis this network is poorly developed and mainly procambial, but in the fruit it forms a coarse reticulum of thickened bundles over the surface of the bony endocarp. Above the locules the dorsal bundles pass upward as the major bundle to the style bases, where they may remain distinct, or unite with the ventrals as a single broad vascular arc.

In the following descriptions the general morphology of the inflorescence and flowers of each genus is discussed, followed by a description of the vascular anatomy. Abbreviations for various organs and anatomical features illustrated in the figures are introduced as necessary in the text. In the absence of petals, and due to the uncertain morphological origin of the perianth in some genera, the terms *perigon* and *tepal* are used, rather than calyx and sepal. An appendicular hypanthium consisting of fused sepal, stamen, and petal bases is present in the petaliferous genera of Hamamelidoideae, but is absent in certain apetalous genera (*Distylium*, *Molinadendron*, *Matudaea*), or is replaced by an analogous structure, possibly consisting of foliar, axial, and floral tissues united in a cup around an ovary. This structure, which has not previously been investigated, is here referred to as a *hypanthium* for the sake of simplicity. But, as seen in *Sycopsis dunnii*, staminate flowers may occur at various levels on its outer wall or on its rim, in which case the term "hypanthodium" [1] in the sense of Emerson & Emerson (1960) might be more appropriate. The shallow floral cups in the flowers of *Parrotia*, *Fothergilla*, and *Parrotiopsis* may be of similar origin, although this is not known for certain, and they are also termed *hypanthia*. The term *stele* is used here in a general sense with reference to the vascular system of the peduncle, pedicel, and receptacle, and may include both primary and secondary tissues. The terms *bundle*, *trace*, and *strand* are used interchangeably. The term *trunk bundle* is applied to those vascular bundles which traverse the hypanthium longitudinally, and branch distally to supply traces to the perianth and androecium.

OBSERVATIONS AND INTERPRETATIONS

1. **Distylium** Siebold & Zuccarini, Fl. Jap. 1: 178. *t. 94*. 1841.

FIGURES 1–3, 4A–D.

The widespread but poorly understood Asian genus *Distylium* contains about 11 species of evergreen shrubs and trees distributed in temperate, subtropical, and tropical regions from Japan and southern Korea southward to Taiwan, eastern and southeastern China, westward in the Himalaya to Assam, and southward through Burma, Indo-China, and Malaya to Java and Sumatra (Walker 1944; Airy-Shaw 1963; distribution map in Balgooy, 1966). Three Central American species originally ascribed to this genus were recently segregated as the genus *Molinadendron* Endress (1969).

The complexities associated with the variation and reduction of flower and inflorescence in *Distylium* are such that it is difficult to consider one without the other, for it is often difficult to distinguish between flower (euanthium) and inflorescence (pseudanthium), or between vegetative

[1] Eames (1961, p. 249) notes that the term hypanthium has been loosely used to cover "complex and varied" morphological structures. Jackson (1928) lists both hypanthium and hypanthodium, with the definition "an enlargement or development of the torus under the calyx; a syconium." Emerson & Emerson define hypanthodium as "an inflorescence with concave capitulum on whose walls the flowers are arranged."

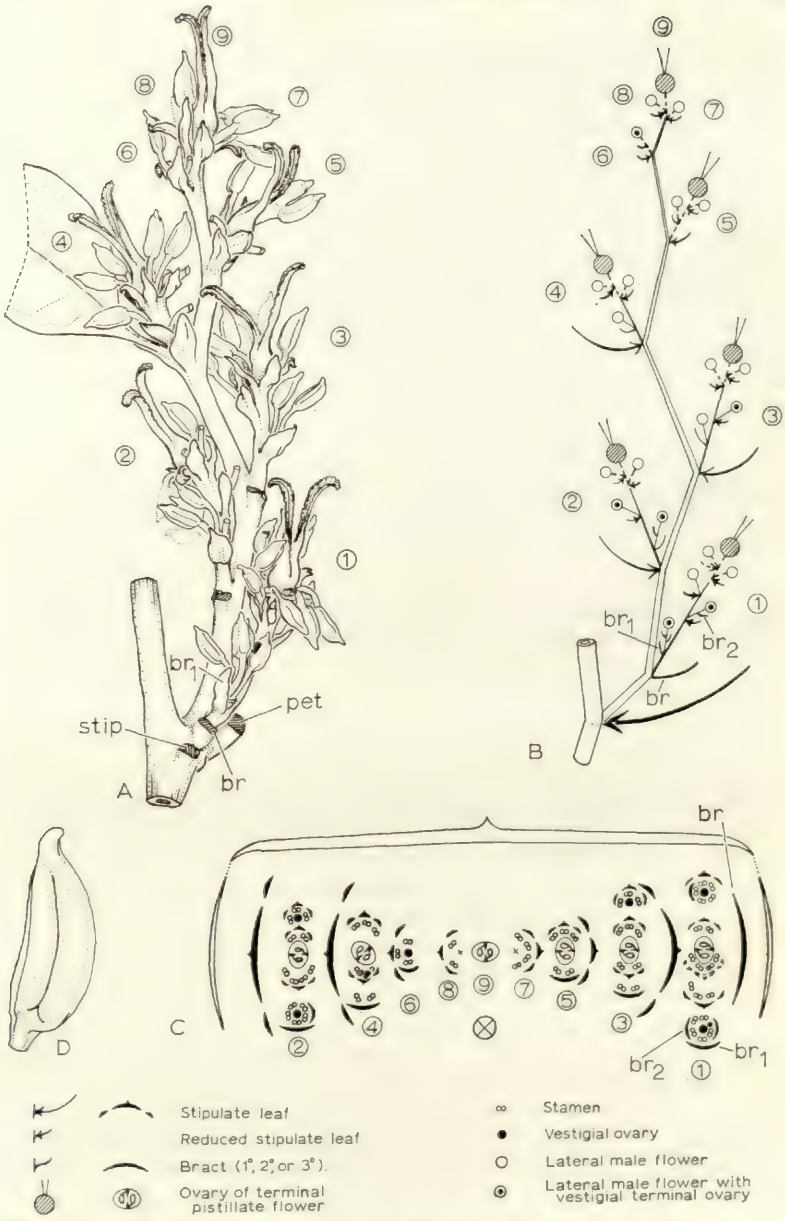

FIGURE 1. **Distylium racemosum:** A-C, structure of a complex inflorescence, showing stages of reduction in leaves, bracts, and lateral inflorescence units. Each unit is designated by the same number in all three figures; A, inflorescence at anthesis, some bracts and anthers removed — note terminal position of functional ovary in each unit; B, diagrammatic representation of A; C, inflorescence diagram of A; D, anther — solid line marks path of dehiscence.

axis and inflorescence axis. The inflorescence of *Distylium racemosum* is, therefore, discussed in some detail. The following descriptions and interpretations of the infloresence and floral morphology are based primarily on material of *Distylium racemosum* Sieb. & Zucc., *D. gracile* Nakai, and *D. stellare* O. Ktze. in my collections, but I have also examined available herbarium specimens of other species of the genus, and find no morphological evidence to contradict the interpretation.

MORPHOLOGY: The inflorescences of *Distylium* are small, bracteate, axillary or terminal spikes, racemes, or panicles, produced from a bud of the previous or current growth season (FIGURES 1, 4). The flowers are naked (Vink 1957) and unisexual, but through aggregation of staminate and pistillate flowers often appear bisexual, with a functional or abortive ovary. The stamens at maturity are strongly exserted, with oblong to ovate, dark-red anthers in which the connective is produced as a short apiculus, and dehiscence is slightly dorsi-lateral by means of longitudinal slits which are simple in some species and basally subvalvate in others (FIGURE 1D). The functional ovaries are terminal on the inflorescence axes and are very small at anthesis, with exserted, straight to recurved styles. A hypanthium such as that found in most genera of the family is never present.

A compound inflorescence of *Distylium racemosum* ($n = 12$, Sugiura 1936), containing several axillary inflorescence units arranged along a short lateral axis, is illustrated in FIGURE 1A, and diagrammatically in FIGURE 1B and C. Examination of each of the inflorescence units reveals a variety of vegetative and floral modifications and reductions such as those noted by Hemsley (1907) and by Vink (1957), as follows: inflorescence unit number 1 is axillary to a large bract (br, excised in FIGURE 1A, but scar area hatched); units 2, 3, and 4 are axillary to well developed stipulate leaves, such as that figured with unit 4 (excised at 2 and 3, scar areas hatched); units 5, 6, 7, and 8 are axillary to trimerous bract groups which continue the two-ranked phyllotactic pattern of the lower nodes and represent reduced stipulate leaves; unit 9 is represented only by the terminal ovary.

Within unit 1, in ascending order: the proximal node bears a primary bract which encloses two secondary bracts inserted oppositely in the transverse plane, flanking a male flower containing six stamens (one of them sterile) and a tiny abortive ovary; the second node bears a trimerous bract group to which is axillary a small, transversely inserted secondary bract, a flower consisting of five stamens, and an abortive ovary; the third node bears a trimerous bract group with three stamens in the axil, but no secondary bracts and no ovary; the inflorescence appears to terminate with a set of trimerous bracts unilaterally inserted at the base of a well developed, functional ovary which is surrounded basally by a cycle of six irregularly inserted stamens, two of which are more or less axillary to the bracts, while the other four are inserted on the receptacle around the naked side of the ovary. In the systematic literature this terminal group of bracts, stamens, and ovary would be interpreted as a bisexual flower with

three sepals, but morphological and anatomical evidence indicate that the bract group and its associated stamens represent a fourth node, that the remainder of the stamens represent a fifth node at which the bracts have failed to develop, and that the ovary represents a terminal, naked pistillate flower. Bracts such as those which I interpret as abortive at node five (indicated by dashed symbols in FIGURE 1B–1, C–1) are actually present at the tips of inflorescence units 2, 3, and 4. In the material available, all stages of reduction of such bracts can be found, down to three abortive primordial protrusions on the receptacle on the naked side of the ovary. The interpretation of the ovary as a terminal, naked, pistillate flower is based on vestigial vasculature in its base (described below), which suggests the former presence of a hypanthium or floral envelope of some sort in the recent phylogenetic history of the genus.

Each higher inflorescence unit is progressively more reduced than unit 1, with fewer bracts and flowers. Unit 5, for example, is axillary to a trimerous bract group and consists of a functional ovary surrounded by five hypogynous stamens and four bracts of varying size. But one of the bracts is obviously larger, is inserted opposite and morphologically lower than the other three in the transverse plane, and bears two fertile stamens in its axil, while three stamens are associated with the opposing bract group. This inflorescence would also be described as a bisexual flower, but actually consists of two lateral, naked staminate flowers and a terminal, naked pistillate flower. Unit 6 consists of single primary bract and three fertile stamens, representing a naked staminate flower associated with an abortive terminal ovary. Units 7, 8, and 9 are aggregated as a terminal group of six bracts, six "hypogynous" stamens, and a terminal functional ovary. But three of the bracts, with four associated stamens, morphologically lower and opposite the others on the axis, represent an inflorescence (unit 7) reduced to a naked staminate flower axillary to a bracteate stipulate leaf. Unit 8 is similarly reduced to two stamens axillary to the three higher bracts, and the ovary, designated as unit 9, represents a terminal, naked pistillate flower. Units 7, 8, and 9 thus duplicate the condition apparent at the tips of units 2, 3, and 4, with six bracts, five or six stamens, and a functional ovary forming what has generally been considered an incomplete, bisexual flower, a condition brought about by the reduction of leaves and distal internodes of the inflorescence axes, resulting in the aggregation of naked unisexual flowers and their associated subtending bracts to form a bisexual pseudanthium.

More complicated flowering branch systems have been seen in which the lateral axis illustrated in FIGURE 1A would represent only one of numerous progressively reduced units arranged along an axis which terminates in a similar pseudanthium. In such a system branches to the fourth order are involved, each terminating in a pseudanthium, each pseudanthium incorporating elements of two orders of branching.

The terminal position of the functional ovaries and the reduction of subterminal units are more clearly demonstrated in FIGURES 4A–D, of *Distylium racemosum*. FIGURE 4A illustrates an axillary, paniculate in-

florescence bearing seven maturing terminal ovaries subtended by trimerous bract groups. The stamens have fallen away from all the lateral staminate flowers, in some cases, revealing abortive ovaries. A subterminal ovary reduced to one carpel and an abortive bicarpellary ovary (ab ov) are shown in FIGURE 4B and C, while a tricarpellary ovary with an abortive organ protruding from its side is illustrated in FIGURE 4D. The protruding organ is probably a stamen which has become adnate to the ovary and developed a small stigma-like structure terminally. I have found, in my material, several isolated examples of such monstrous stamens consisting of part anther and part stigma, associated with terminal ovaries.

In inflorescences from flowering specimens of *Distylium buxifolium* (Hance) Merr. (*E. H. Wilson 115*, *3537*, [A]) the inflorescence units were found to be spirally arranged rather than two-ranked as in *D. racemosum*, and much reduced from the condition seen in the latter, with shorter, more congested primary axes, fewer nodes and lateral flowers, considerable modification and fusion of the primary and secondary bracts, and pseudanthial complexes containing from 4 to 10 bracts (for the most part in obvious groups of three, and representing the reduced stipulate leaves of possibly 2 to 4 subterminal nodes) surrounding the subterminal staminate and terminal pistillate flowers. An abortive subterminal ovary may be present among the stamens axillary to the morphologically lowest group of bracts in the terminal complex.

ANATOMY: The vascular supply to the petiole of the foliage leaf and to the inflorescence bracts of *Distylium racemosum* and *D. gracile* consists of three traces derived from three gaps in the stele, with a single trace provided to each stipule from the adjacent lateral leaf trace (FIGURE 2A).

FIGURE 2. Steps in the reduction of the vascular supply to the inflorescence bracts of *Distylium racemosum* and *Sycopsis dunnii*: A, typical three trace, trilacunar node of the stipulate leaf; B, lateral traces to petiole vestigial; C, lateral traces absent, only the stipules supplied from the lateral gaps; D, stipulate leaf reduced to a single bract receiving one trace from one gap.

Within the flowering branch system reduction of the leaf blade is accompanied by a corresponding reduction in the vascular supply to the petiole. Reduction of the lamina results first in the failure of the lateral traces to the petiole to develop fully, as indicated in FIGURE 2B, where the lateral traces supply traces to the stipules, then end blindly as vestigial stubs in the cortex near the petiole base. The petiole then receives only a single median trace. Further reduction of the lamina results in the loss of the vestigial stubs, so that only the stipules receive traces from the

lateral gaps in the stele (FIGURE 2C). The bracteate blade may fuse with the stipules to form a single broad, trifid bract, or the leaf blade may be lost and the persistent stipules may fuse into a single bifid bract. The penultimate stage of reduction is a single bract supplied by one trace from one gap. The latter condition is encountered most frequently at the base of an axis (FIGURE 2D).

In view of the great variation in the flowers of *Distylium* I have based the following anatomical description on a selected specimen which I think exhibits the general morphological and anatomical features of the species which were available for anatomical study. FIGURE 3A illustrates the tip of an inflorescence of *D. racemosum* which is similar to those described above except that here the leaf blades at the subterminal nodes are fully developed rather than bracteate. Group 1 consists of a naked staminate flower of four stamens axillary to a leaf. Group 2 looks like a terminal bisexual flower, but consists of two or three stamens axillary to the distal leaf, while the remaining stamens inserted on the naked side of the receptacle (one with a partially laminar anther) are interpreted as referable to a third node (not numbered), the bracts of which have failed to develop. The axis terminates in the terminal ovary.

At the base of group 1, in the wake of the departing leaf traces (lf tr), a small axillary stele (ax 2) is pinched off from the main axis to supply the base of the sessile staminate flower. At anthesis this stele is largely procambial, with scattered protoxylem elements apparent only in polarized light. As the stele ascends in the receptacle four large collateral bundles (st) organize (FIGURE 3C, D, E). Scattered protoxylem strands lying between these bundles in the stele gradually die out, leaving only procambial arcs (stippled) which die out as the four stamen traces depart.

At the base of the distal complex, after the departure of the leaf traces, the stele consists of a ring of numerous collateral bundles. Five more or less equally spaced stamen traces (st) differentiate, then arch outward to enter the bases of the filaments (FIGURE 3F–H). The gaps left by the traces are shortly repaired as the stele consolidates in the receptacle. Although the stamens are inserted at the base of the ovary morphologically, their traces originate well down in the axis anatomically, as much as 500 micra below the ovary base. In longitudinal sections and cleared specimens the ovary appears to be subtended by a relatively long vascular cylinder or stipe (stp in FIGURE 3O, stamen traces and scars not shown in the receptacle).

In the base of the ovary, at a level slightly above the insertion of the filaments, the tips of numerous small, recurved, procambial strands (peri) are encountered in the cortex. When followed upward these can be seen to branch or anastomose to a slight extent before connecting with conspicuous large reflexed bundles which originate from the receptacular stele at the base of the gynoecial supply (FIGURE 3G–I). Although most of this peripheral system appears in the base of the ovary below the locules, some branches of it continue upward and end blindly in the ovary walls above the level of the locule bases (FIGURE 3J–L, O).

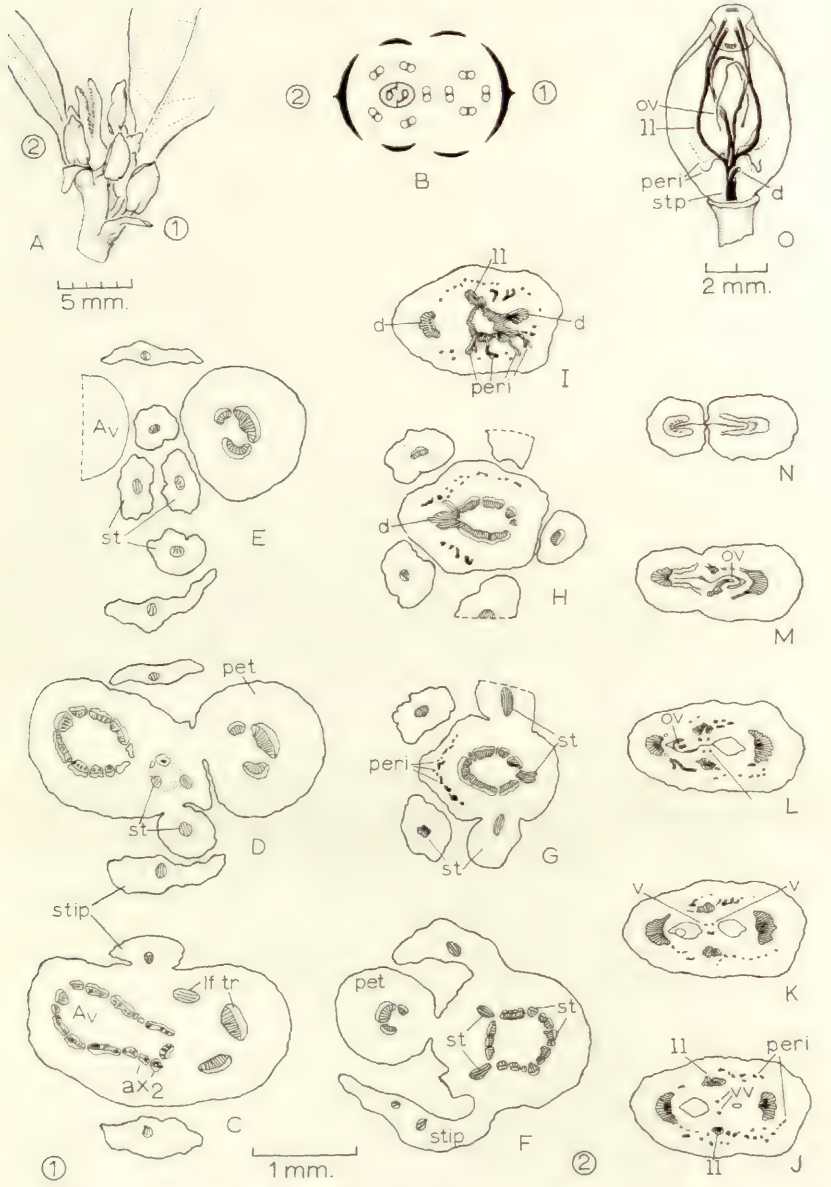

FIGURE 3. **Distylium racemosum:** A, tip of an inflorescence — group 1 is a subterminal staminate flower, group 2 a terminal bisexual pseudanthium — note the stipulate leaves subtending each "flower"; B, diagrammatic representation of A; C-E, transverse sections through group 1 (slightly oblique); C, departing leaf and stipule traces — secondary axis developing; D, stamen traces developing in and departing from the secondary axis; E, stamen filaments in axil of leaf;

In the base of the ovary the receptacular stele is slightly elliptic in transverse sections, with its long axis in the plane of the dorsal bundles. From the median sides of the ellipse broad dorsal carpel bundles (d) depart, along with adjacent bundles of the peripheral system (FIGURE 3H, I). At a slightly higher level two compound lateral bundles (ll) organize on opposite sides of the stele in the transverse plane and diverge slightly toward the periphery (FIGURE 3I, J). The stele then constricts to form a narrow procambial cylinder at the base of the locules, which divides in the median plane to form two procambial compound ventral bundles (vv) in the base of the septum.

The dorsal bundles ascend in the ovary as broad vascular arcs. The compound laterals dichotomize transversely at about the level of ovule insertion near the top of the locules. The compound ventral bundles are not entirely developed at anthesis, and those portions which are present are entirely procambial. They appear to die out as they ascend in the base of the septum, but reappear at a slightly higher level as four individual ventral bundles (v, FIGURE 3J–L). This discontinuity in their development suggests that their differentiation proceeds both acropetally and basipetally in the developing septum. Near the top of the locules the ventrals approach and fuse with their adjacent lateral bundles (l), but the ventral bundle of each fertile margin branches just prior to fusion to provide a trace to the solitary ovule (ov).

The most striking features in the floral apparatus of *Distylium* are the extreme variation in the external morphology of the inflorescences and flowers, the foliar nature of the inflorescence bracts, the development of bisexual pseudanthia, and the curious system of vestigial vascular bundles, here referred to as the peripheral system, in the base of the ovary. The flowers of the genus have not previously been studied anatomically, but have been variously interpreted by systematic workers as polygamous, or as unisexual and monoecious, or as andromonoecious, with a variable number (0–6) of free and unequal sepals (or bracts, or bracteoles) inserted at different levels, an irregular number (2–8) of hypogynous stamens, and a superior ovary (Bentham & Hooker 1865; Baillon 1874; Niedenzu 1891; Harms 1930; Walker 1944; Vink 1957). The gynoecium of *Distylium* has long been considered a prime example of the superior ovary in a family generally characterized by half-inferior ovaries.

Hemsley (1907) described each of several flowers from two inflorescences of *Distylium chinense* Hemsl. in detail, and could find no uniformity in their organization, nor any way to differentiate between the various "bracteoles" and "sepals." He concluded that the flowers of

F-N, transverse sections (slightly oblique) through group 2; F, stamen traces departing the stele; G, stamens separating — vestigial peripheral bundles appearing in the base of the ovary; H, carpel dorsal bundle and adjacent peripheral bundle departing the receptacular stele; I, several peripheral bundles and second dorsal bundle departing from the stele; J, base of locules — some peripheral bundles still evident; K, ovary — individual ventral bundles appearing; L-M, insertion of ovules; N, style bases; O, gynoecial vasculature as seen in a cleared ovary (semi-diagrammatic).

the genus are functionally either male or female, but never hermaphrodite. Walker (1944) states that "the variations in the floral parts between one species and another are so little, or so inconsistently variable that they are of scant use in differentiating species . . ." "It is often difficult to determine whether flowers are unisexual or bisexual, because there may be found stamens and pistils of all degrees of development even in the same inflorescence."

Vink (1957) noted that the floral bracts of *Distylium stellare* most often occurred in threes and sixes, and that the middle bract of a group of three sometimes was leaf-like in appearance, while the two lateral bracts were always more or less lanceolate in shape. Since the leaves of the genus are stipulate, he interpreted the bracts as reduced stipulate leaves, and concluded that the flowers of *Distylium* are asepalous, as well as apetalous. His is the only interpretation of the inflorescence bracts which is supported by the anatomical evidence. He also observed that distal flowers are often merged in twos, forming "twin flowers" at the tips of the inflorescences.

Croizat (1960, 1964) rejects any conventional explanation for the inflorescence bracts and floral organization of *Distylium*, considering the flowers of the genus exemplary of his proposed transitional stage of "flower making" between a unisexual amentiferous inflorescence and a bisexual angiospermous flower. He considers the unisexual flower and inflorescence primitive, and derives the bisexual flower through the "sexualization into maleness" of pistillate flowers by the *de novo* origin of stamens on scales (the "sepals," "bracts," "bracteoles" of *Distylium*) subtending the pistils. These stamens supposedly assume the functions of the male inflorescences which are then suppressed. However, I find no evidence in my material of a unisexual staminate inflorescence of the type figured by Croizat (1960, p. 296, *fig. 36A*). The "twin flowers" mentioned by Vink are interpreted by Croizat (1960) as "Scales ("carpels") originally arranged to establish two separate floral structures . . . here rearranged to establish one only, thus factually marking the final transformation of an inflorescence into a single flower." Morphologically and anatomically, "twin flowers" are nothing more than two bisexual pseudanthia, one terminal the other subterminal, closely associated at the tip of an inflorescence. Each is subtended by a trimerous bract group, stamens of both are inserted between the two pistils, and vestigial peripheral bundles are present in both ovaries. Although Croizat was correct in his interpretation of the pseudanthial nature of some "flowers" in *Distylium*, the evidence now available contradicts his views concerning the method of their derivation.

2. **Sycopsis** D. Oliver.[2] Trans. Linn. Soc. London 23: 83. 1860.

FIGURES 4E–F, 5, 6.

An Asian genus of evergreen shrubs or trees containing about nine species ranging in distribution from Assam through Southeast Asia and

[2] The generic name is derived from the Greek *sykos*, for fig, and *opsis*, meaning

the Malay Archipelago to New Guinea. *Sycopsis sinensis* Oliv. has the most northerly distribution, occupying a broad east-west band across seven provinces of central China, while *Sycopsis dunnii* Hemsl. has a very broad southern distribution from southern China southward to Sumatra and eastward to the Philippines and New Guinea. The other seven species have relatively restricted distributions. Prominent among them are *S. griffithiana* Oliv. in Assam and possibly Yunnan, *S. laurifolia* Hemsl. in Yunnan, *S. tutcheri* Hemsl. in Kwangtung (Hong Kong) and Hainan, and *S. salicifolia* H.-L. Li in Walker, in Hainan.

Only *Sycopsis sinensis* is well known in cultivation, and it has recently been shown to be interfertile with *Parrotia persica*, although the hybrid, × *Sycoparrotia semidecidua*, is apparently sterile (Endress & Anliker 1968).

The following descriptions are based primarily on flowers and inflorescences from cultivated plants of *Sycopsis sinensis*, and from herbarium specimens of *S. dunnii* and *S. laurifolia*, but available specimens of the several other species were also examined morphologically.

Morphology: The inflorescences of *Sycopsis* are short, axillary or terminal panicles, spikes or heads. The congested spikes or heads of *Sycopsis sinensis* (Figure 6n) and *S. griffithiana*, with each flower enclosed by a broad, densely dark-brown-hirsute primary bract, differ significantly from the short open spikes or racemes of *S. dunnii* and related species, with flowers subtended by unilaterally inserted trimerous groups of small bracts (see Figure 4e–h). Secondary bracts are generally absent in the inflorescences, but one or two may occur flanking a basal flower, either free or partially adnate to the hypanthium.

The axillary or terminal flowers are sessile to subsessile, asepalous (Vink 1957) and apetalous, and appear to be andromonoecious (I have found no evidence of strictly pistillate flowers that would substantiate the interpretation of polygamous inflorescences encountered in the systematic literature). Staminate flowers contain 3 to 7 stamens in *Sycopsis dunnii*, and (5–)7 to 10 in *S. sinensis*, inserted perigynously in a single cycle on the rim of a rudimentary, hirsute, naked (*S. dunnii*) or irregularly toothed and lobed (*S. sinensis*, Figure 7a) hypanthium, around a minute abortive ovary. At anthesis the stamens become strongly exserted, with elliptic to ovate (*S. dunnii*, *S. laurifolia*) to distinctly oblong (*S. sinensis*), 2-celled anthers containing four pollen-sacs, and dehiscing by means of lateral longitudinal slits which are simple above, but ventrally subvalvate below. The anther connective is produced as a short, blunt point. Bisexual flowers contain a 2(–3)-carpellary, superior to slightly semi-inferior ovary, surrounded by an urceolate to subglobose hypanthium which, in *Sycopsis dunnii* and related species, bears irregular bracts or bract groups (the bracteoles and sepals of most authors) in-

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likeness (Rehder 1954). Oliver (1860, p. 83), in his original description, states that "the young subobovate fruits, narrowed and (from drying?) more or less sulcate below, together with the general appearance of the plant, recall some of the narrower-leaved species of East Indian *Fici*."

FIGURE 4. **Distylium racemosum** and **Sycopsis dunnii**: A-C, *Distylium racemosum*; A, maturing inflorescence, stamens absent — note terminal functional ovaries and a few axillary abortive ovaries; B, pistil of subterminal pseudanthium re-

serted unilaterally at its base, at various levels on its outer surface, and on its often oblique rim. But in *S. sinensis* and *S. griffithiana* there are no unilaterally inserted bract groups, and the level to oblique hypanthium rim bears a single cycle of (4–)5 to 7 irregularly lobed to incised tepals which are basally connate into a tube above the rim (cf. FIGURES 5A and 6A). Three to seven stamens are present in the bisexual flowers of *S. dunnii*, while 8 to 9 stamen scars could be counted on the hypanthium in the post-anthesis flowers of *S. sinensis* which I examined. The long styles are spreading (*S. dunnii*) to spirally curved (*S. sinensis*). A single ovule or seed occupies each locule. In inflorescences of *Sycopsis dunnii* and *S. laurifolia* it appears to me that only the terminal ovary (i.e., in the terminal bisexual flower) on each inflorescence axis is functional. The lateral and subterminal flowers on each axis are staminate through reduction of the ovary. A staminate flower, or an abortive sterile flower, is usually axillary to the bract group at the base of the terminal flower, and stamens may also be axillary to the bract group inserted at mid-height on the hypanthium (FIGURES 4E–H, 5A, C). In *S. sinensis* the ovary of each bisexual flower in the spike may be functional.

The morphological differences between *Sycopsis dunnii* and *S. sinensis* are sufficient to place their congeneric relationship in question. Consequently, the vascular anatomy of both species is considered here.

ANATOMY OF SYCOPSIS DUNNII: Terminal flowers with functional ovaries, associated bracts, and in some cases abortive subterminal flowers, taken from herbarium specimens (*Steward & Cheo, 165, 170, 199*[A]; also *S. laurifolia, A. Henry, 11365*[A]), were sectioned or cleared. The flowers are variable in their organization with regard to the level of insertion of the bracts, and in the number of bracts (0–2) and stamens on the rim. Relatively few flowers of either species were available for sectioning, and the vascular organization of individual flowers differs with their morphological organization. The flowers of *S. laurifolia* appear to agree in general with those of *S. dunnii*.

The vascular supply to the trimerous bract groups subtending the lateral staminate flowers and the terminal bisexual flowers is similar to the nodal anatomy typical of the foliage leaf, i.e., three traces derived from three gaps, supplying the central reduced leaf blade, with a trace supplied to each stipule by the adjacent lateral leaf trace. The vascular supply to the three bracts mounted on the side of the hypanthium may be similar to the typical pattern or represent a reduced modification of it, ultimately consisting of three separate traces, each of which supplies only one bract. The modifications of the vascular supply to the bracts are similar to those described above (FIGURE 2) for *Distylium*. The

duced to a single carpel; C, subterminal pistil abortive; D, three-carpelled terminal pistil — note protruding adnate organ. E-H, *Sycopsis dunnii*; E, maturing inflorescence, stamens absent — note trimerous bract groups on flanks of hypanthia; F, subterminal flower almost fully developed, probably functionally staminate; G, subterminal flower abortive and sterile; H, subterminal flower reduced to a bristle-like appendage (ab fl) adnate to the hypanthium.

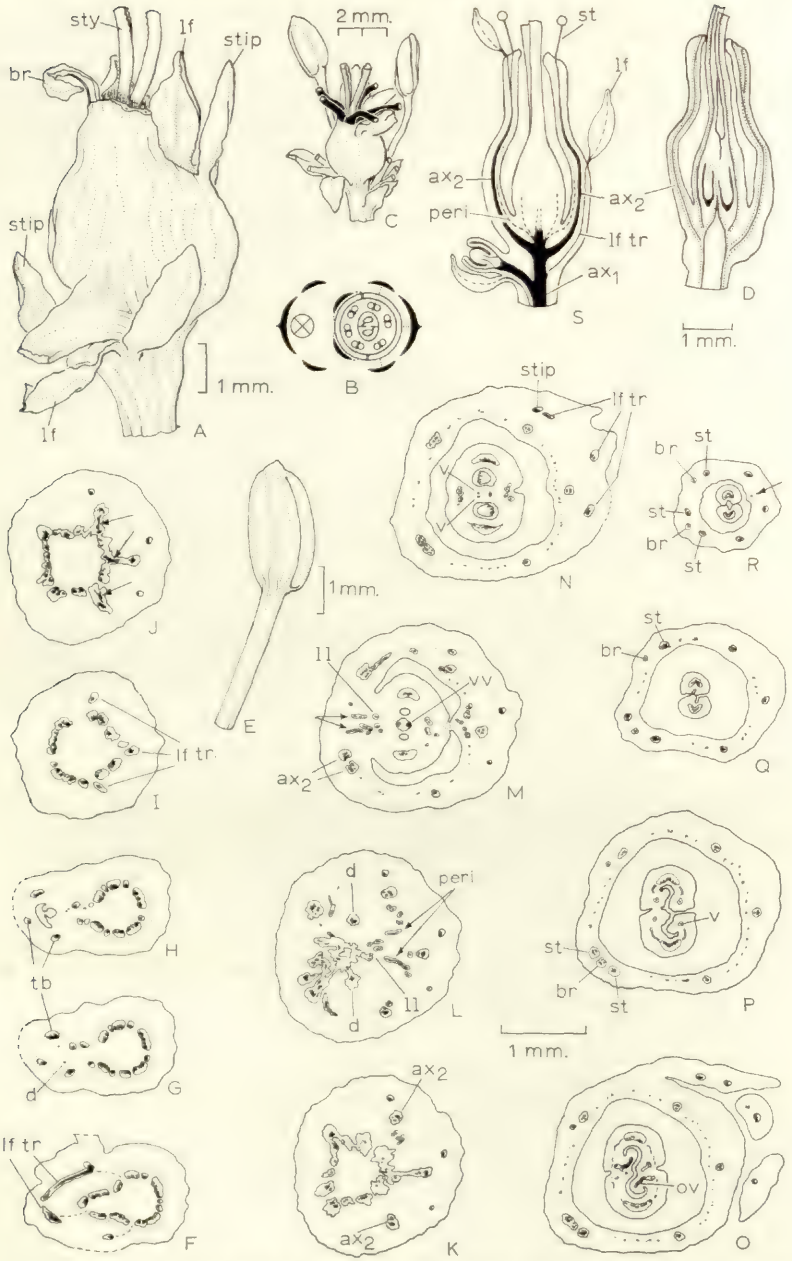

FIGURE 5. **Sycopsis dunnii:** A, view of a terminal bisexual flower and subterminal abortive sterile flower (post-anthesis); B, floral diagram; C, view of an inflorescence tip at anthesis, with two subterminal staminate flowers beneath the

traces supplying bract groups inserted on the side of the hypanthium originate from the peduncular stele well below the departure of the main vascular supply to the hypanthium, and ascend in the parenchymatous tissue near the outer surface of the hypanthium, entirely apart from the remaining vasculature (FIGURE 5I–O). In one instance the trace to a solitary distal bract was discontinuous for a considerable distance in the upper portion of the hypanthium, possibly having been disrupted by elongation of the latter (a phenomenon noted also in *Fortunearia*).

The vascular supply of a single trace to each of the bracts inserted on the rim of the hypanthium is derived within the hypanthium from narrow secondary vascular cylinders or trunk bundles which also supply the stamens and constitute the main vascular supply to the hypanthium. The major supply to the hypanthium develops from the peduncular stele well below the base of the ovary (about 600 to 700 micra below the base of the locules in the sectioned flower of FIGURE 5), where as many as seven large collateral bundles diverge on as many radii into the cortex (FIGURE 5J–L). Immediately behind each of these, and from a slightly higher level as seen in transverse sections, one to three small branches from adjacent bundles bend outward (FIGURE 5J, arrows) and take up positions on the adaxial side of the larger bundle, where they remain distinct through almost the entire length of the hypanthium, uniting with the larger abaxial portion only as the rim is approached and the strands consolidate to form a stamen trace. In transverse sections it appears that the phloem accompanying the small adaxial xylem strands is oriented laterally to adaxially, so that the aggregate of vascular strands in each group then varies in appearance from a narrow, more or less continuous to discontinuous ring of xylem strands with associated external phloem, as in a narrow stele, to two opposing tangential narrow bands of xylem with phloem on the abaxial face of the outer band, and on the adaxial face of the inner band. In some flowers a relatively substantial vascular cylinder occurs in the hypanthium, originating from the peduncular stele approximately in the transverse plane of the ovary (and in the plane of the two-ranked bracts), and ascending to supply traces to bracts and stamens on the rim (FIGURE 5M–R).

From the bases of these trunk bundles and secondary steles lateral

terminal bisexual flower; D, longitudinal median section (semidiagrammatic) of a maturing terminal flower (bracts are out of the plane of section); E, stamen; F-H, sections through the abortive subterminal flower; F, leaf traces and developing secondary stele; G, bundles of abortive hypanthium and carpel dorsal bundles; H, fragment of abortive ovary apparent; I-R, transverse sections through receptacle and terminal flower; I, three leaf traces departing the peduncular stele; J, K, minor secondary axes to the hypanthium leaving the stele; L, peripheral bundles forming on right side; M, base of locules — note larger secondary stele and peripheral bundles on left side; N, about middle of ovary — note stipule trace, distinct ventral bundles on left; O, ovule insertion — note bracts separating from the hypanthium; P, larger secondary axis in the hypanthium has divided into three smaller units; Q, R, upper levels of hypanthium and styles; S, diagrammatic representation of a terminal bisexual "flower" interpreted as a pseudanthium.

branches are given off to either side near the base of the hypanthium. The branches move laterally and upward in the hypanthium, often branching and anastomosing with strands from adjacent bundles. In transverse sections these branches are situated randomly between the major bundles (FIGURE 5M–O). Much of this system dies away as it ascends (at least in the post-anthesis flowers examined), but in some cases a single bundle may persist to the rim of the hypanthium between and slightly adaxial to each pair of major bundles (arrow in FIGURE 5R), suggesting a vestigial supply to abortive stamens. I could find no anatomical evidence in the hypanthium suggesting the former presence of sepals abaxial to the stamens on the rim.

Above the departure of the major bundles to the hypanthium the remaining bundles of the peduncular stele shortly consolidate to form two dorsal carpellary bundles (d), a narrow receptacular stele which enters the base of the septum to form the compound ventral bundles (vv), and two diffuse groups of traces on either side of the receptacle in the transverse plane from which are derived the compound lateral carpellary bundles (ll) centripetally, and centrifugally a series of weak traces (peri) which diverge almost horizontally into the base of the hypanthium just beneath its separation from the ovary, and about 100 to 200 micra higher than the divergence of the major hypanthial bundles (FIGURE 5L, M, S). Within the base of the hypanthium these traces, in association with some minor strands derived from branches of the main hypanthial system, form an irregular ascending, branching, and anastomosing system of bundles in the parenchyma just within the adaxial face of the hypanthium, to either side of the ovary in the transverse plane (FIGURE 5M–P, S). This system also gradually dies away as it ascends. The vascular supply to the hypanthium, therefore, consists of two independent sets of traces derived from different levels in the receptacular stele.

The ovary often appears to be fused with the hypanthium to a slightly higher level on the transverse side which bears the distal bracts (cf. FIGURE 5M). Within the pistil the compound lateral and compound ventral bundles divide in the upper half of the ovary to form distinct laterals and ventrals which fuse at the level of ovule insertion. A single ovular trace departs from the ventral of each fertile margin just prior to its fusion with the lateral (FIGURE 5O).

ANATOMY OF SYCOPSIS SINENSIS:

Bisexual flowers. Post-anthesis flowers from which the stamens had fallen were taken for sectioning from the lower half of inflorescences where there is less crowding of the flowers (cf. FIGURE 6N) and less likelihood of deformation of the receptacular vasculature.

A cylindrical pedicellar stele subtends the flower. In the receptacle 8 to 13 large bundles diverge sharply from the stele to enter the base of the hypanthium, in which they ascend more or less directly to the rim. Some of the bundles function only as traces to the shallow perigon tube and its irregular lobes, while others are trunk bundles supplying traces

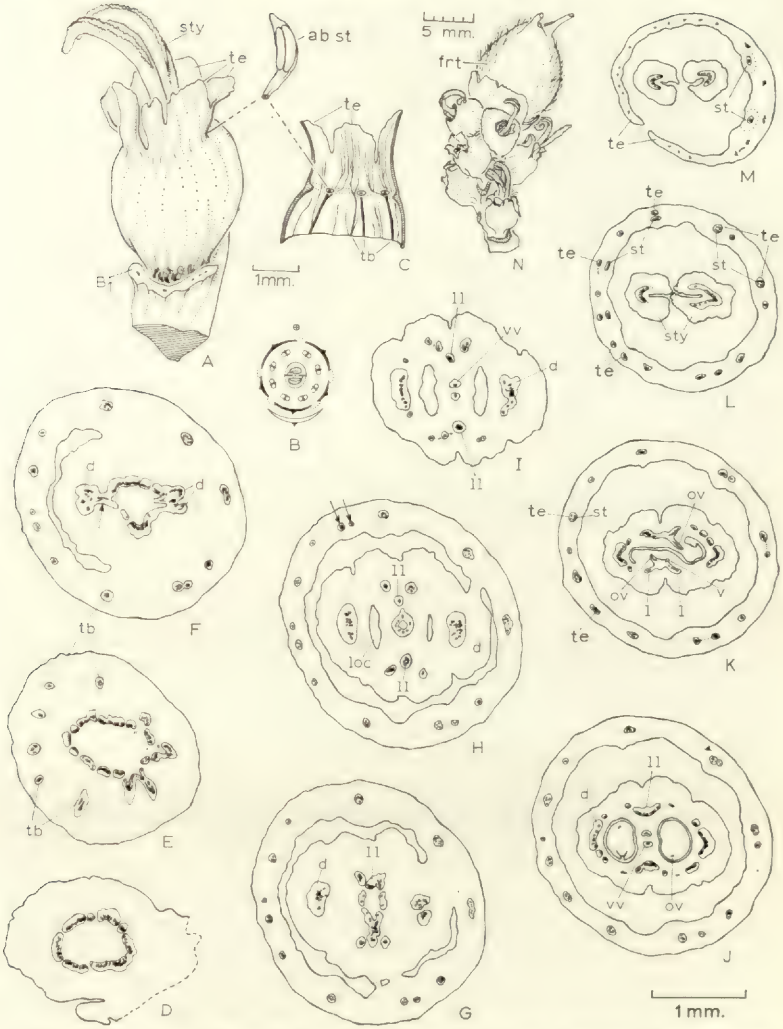

FIGURE 6. **Sycopsis sinensis** (bisexual flower): A, post anthesis flower — note irregular lobing of the perianth tube, one sterile stamen shown; B, floral diagram; C, drawing from cleared portion of the mature hypanthium showing perianth lobes, stamen scars, trunk bundles, irregular vasculature of the lobes; D-M, transverse sections of post-anthesis flower; D, pedicellar stele and base of primary bract; E, receptacle — note departing hypanthial trunk bundles and part of receptacular stele; F, base of ovary, carpel dorsal bundles forming; G, base of ovary, compound lateral bundles forming; H, base of locules — note residual receptacular stele in base of septum; I, slightly above locule bases — note compound ventral bundles; J, mid-height in ovary; K, insertion of the ovules; L, formation of tepal and stamen traces in hypanthium; M, insertion of stamens on the hypanthium rim; N, fruiting inflorescence, only terminal flower in fruiting condition — note splitting hypanthium.

to both stamens on the rim and to the tepals. At various levels in the hypanthium the trunk bundles may produce single lateral branches which function as dichotomizing traces to the perigon (cf. FIGURE 6C), but branching is sparse within the hypanthium. I could find no regular patterns in either the lobation of the perigon, or in its vascularization.

In transverse sections some of the hypanthial bundles are collateral, while others, particularly the trunk bundles, are somewhat variable, often appearing as narrow vascular cylinders as in the hypanthium of *Sycopsis dunnii*. There is no evidence, however, of the two systems of numerous minor bundles derived from branches of the trunk bundles and from the receptacular stele in the vicinity of the developing componnd lateral carpellary bundles, as in *S. dunnii*.

Occasionally a discontinuous vascular bundle, such as those indicated by arrows in FIGURE 6H, appears in the hypanthium. In this particular instance the larger bundle was about 500 micra long, while its smaller companion was only about 80 micra long. Both ended blindly above and below.

Slightly below the level of stamen insertion many, but not all, of the trunk bundles divide tangentially. The adaxial branch (st) enters the base of a stamen, while the outer branch (te) enters the base of the perigon tube, where it dichotomizes irregularly, forming 2 to 3 smaller bundles which supply the tepal lobes (FIGURE 6C, K–M).

Above the departing hypanthial bundles a prominent receptacular stele continues upward for a short distance (about 200 to 350 micra in the post-anthesis material examined), becoming broadly elliptic in the median plane in transverse sections as the dorsal carpellary bundles (d) organize and depart. As each dorsal moves away from the stele one or two median or lateral traces from it bend sharply inward and return almost horizontally toward the stele (arrow in FIGURE 6F), where they are incorporated into a smaller vascular cylinder remaining at the center of the receptacle. From this cylinder two to four bundles depart on either side in the transverse plane to take up positions in the bulging walls of the exocarp and on the edges of the septum as lateral bundles (l) or diffuse compound lateral bundles (ll, FIGURE 6G–I). Their departure leaves two small opposing vascular arcs in the median plane which consolidate to form a narrow, largely procambial receptacular cylinder containing several strands of protoxylem in the base of the septum (FIGURE 6G–H). At the base of the locules the hypanthium is essentially free from the superior ovary, and the major bundles of both are apparent in transverse sections.

Within the ovary the dorsal bundles are relatively massive and occupy prominent dorsal bulges in the carpel walls. In the bundle groups at either edge of the septum the central bundles function as the compound laterals, while the lateral bundles move outward into lateral bulges and eventually ramify and anastomose into the vascular networks of the carpel walls. The narrow receptacular cylinder in the base of the septum shortly divides to form two compound ventral bundles which ascend unbranched

to the base of ovule insertion where each dichotomizes. The distinct ventrals thus formed then fuse with adjacent distinct lateral bundles. The ovule traces are supplied from the ventrals just prior to fusion (FIGURE 6J, K). In some ovaries it appears that the ventral bundle of the fertile margin goes entirely to the ovular funiculus, free of any connection to the adjacent lateral bundle, but such connections may form later in the ontogeny of the ovary. The marginal ventral bundles in each style soon become associated with the dorsal bundle to form a vascular arc, rather than three distinct bundles (FIGURE 6L, M).

Staminate flowers. The hypanthium is strongly reduced, and the gynoecium rudimentary in the sessile staminate flowers (FIGURE 7A). The shallow, membranaceous perigon tube which projects above the rim of the hypanthium is irregular in its lobing and vascularization. The lobes bear long dark-brown stellate hairs on their distal margins. The tepals indicated in the floral diagram (FIGURE 7B) correspond to the lobes of the perigon tube as they appeared in the sectioned flower illustrated.

A well organized pedicellar stele was present in some, but not all of the specimens examined. A reduced pedicellar stele may be present only as a lobe of the peduncular stele on the lower side of the flower, while on the upper side the bundles to the receptacle originate from the margins of a gap in the peduncular stele.

In the receptacle of the flower the entire stele is incorporated into 9 to 12 large bundles, most of which enter the hypanthium (FIGURE 7C-E). In the median plane two dorsal carpel bundles (d) are derived either from a single bundle of the stele, or by the fusion of 2 to 3 traces from adjacent hypanthial bundles (FIGURE 7E, F). No compound ventral or lateral carpel bundles are formed, but there is frequently the appearance of vestigial traces to such bundles in the form of protoxylem strands which bend inward from the bundles in the receptacle at the level of dorsal bundle formation.

The ascending bundles in the shallow hypanthium may remain entire, or give rise to one or two lateral branches which eventually supply the perigon tube (FIGURE 7H). The trunk bundles, situated on the radii of the 7 to 10 stamens, branch just below the insertion of the stamens to produce a large adaxial stamen trace (st), and a smaller abaxial trace (te) which enters the perigon tube, where it may divide irregularly and supply branches to a tepal. A few (1 to 3) bundles in the hypanthium divide at about the level of stamen insertion to provide traces to the perigon only. There was no correlation between the number of bundles in the hypanthium and the number of stamens on its rim in the flowers examined.

In *Sycopsis*, as in *Distylium*, it becomes difficult to distinguish between flower and inflorescence. The flowers, especially, present problems of interpretation and nomenclature, particularly the tubular structure surrounding the ovary and bearing the stamens. This has been termed an urceolate receptacle (Harms 1930; Tong 1930; Walker 1944; Vink 1957), a hy-

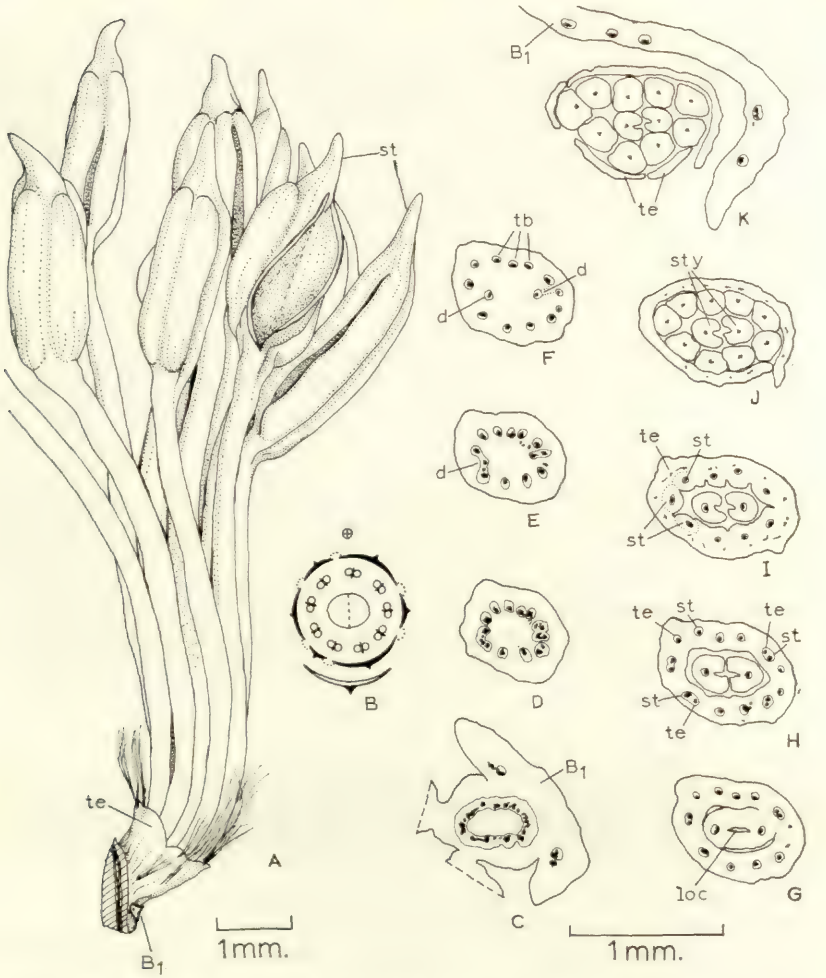

FIGURE 7. **Sycopsis sinensis** (staminate flower): A, flower at anthesis — note irregularly lobed syntepalous perianth; B, floral diagram; C-K, transverse sections of a flower at anthesis; C, pedicellar stele and primary bract (bract omitted in figures D-J); D, expanding pedicellar stele; E, receptacle — note developing carpel dorsal bundles; F, receptacle — note hypanthial trunk bundles and carpel dorsals; G, rudimentary, unilocular ovary and separating hypanthium; H, hypanthial trunk bundles dividing to form perianth and stamen traces; I, insertion of stamens on hypanthium; J, through the perianth tube, filaments, and styles; K, separation of some tepals and upper portion of the primary bract.

panthium bearing calyx lobes (Endress & Anliker 1968, ref. *S. sinensis*), or a calyx tube with short lobes (Oliver 1860; Niedenzu 1891).

The nature of the perianth has also proved problematical. Hemsley (1907), in his original descriptions and illustrations of *Sycopsis dunnii*,

S. tutcheri, and *S. philippinensis* (= *S. dunnii*), clearly indicates the unilateral insertion, variability in number, and morphological similarity of the "bracteoles" of the inflorescence and the "sepals," counting as the latter the 1 to 3 bracts occurring on the hypanthium rim. The variability in the numbers of sepals is also evident in the species descriptions in Walker's (1944) revision of the genus. Vink (1957), in his comparative notes on the flowers and bracts of *Distylium stellare* and *Sycopsis dunnii*, concluded that the flowers of *Sycopsis* are also asepalous, and that the usually trimerous bract groups at the base, sides, and rim of the urceolate hypanthium are actually reduced stipulate leaves. The vascular supply to the bract groups, described above, clearly indicates that his interpretation is correct, at least for *S. dunnii* and *S. laurifolia*. The foliar nature of the tepals of *Sycopsis sinensis* and *S. griffithiana* is not so clear cut, however. In these species the 5 to 7 tepals are inserted in a single cycle on the rim of the hypanthium, projecting beyond the rim as an irregularly lobed and fused perigon tube. Oliver (1861), in his original description of the genus, based on *S. griffithiana*, states of the perianth "it is doubtful how far the lobation and degree of obliquity of the calyx limb is constant." He later (1890) described the perianth of *S. sinensis* as "calycis tubo irregulariter fisso." Vink's interpretation of the bracts of *S. dunnii* does not appear directly applicable to the markedly different perianths of these two species.

Interpretations of the sexual condition of the flowers have varied. Oliver described the flowers of *S. griffithiana* as unisexual through abortion, and questioned whether they were ever hermaphrodite. Walker found the flowers of the genus to be "unisexual and monoecious or andromonoecious," while Vink considered them "polygamous monoecious." In cultivated specimens of *Sycopsis sinensis* Endress (Endress & Anliker 1968) found only bisexual and staminate flowers (i.e., andromonoecious). He observed that the buds of all flowers are bisexual, and that the stamens develop in all flowers, but that the ovary is abortive in many. The pistillate flowers reported in the literature actually represent bisexual ones from which the stamens have fallen. He also found that inflorescences terminal on short or long shoots contained mostly bisexual flowers, with only one or two basal staminate flowers, while inflorescences from lateral buds were in many cases entirely staminate and soon deciduous.

Stamen development is often irregular in bisexual flowers of *Sycopsis sinensis* with several stamens abortive. This condition has also been noted in *S. griffithiana* by Oliver (1860), and in the generic description by Vink (1957, presumably for *S. dunnii*). Walker noted that the hypanthium does not develop and enlarge with the fruiting ovary, as do the hypanthia of other genera of the family, but splits irregularly almost or quite to the base, forming a shallow 2- to 3-valved cup around the base of the mature fruit (FIGURE 6N, terminal fruiting flower). In *S. laurifolia*, however, as in *Sinowilsonia*, the hypanthium does appear to develop with the fruit, forming a thin papery urceolate covering which ruptures only as the woody capsule within springs open.

The morphology and anatomy of *Sycopsis dunnii* and *S. laurifolia* indicate that their floral apparatus is rather specialized. Such morphological features as the open spicate to paniculate inflorescences; the terminal position of the functional ovaries; the reduction of lateral flowers to a staminate condition; the form and dehiscence of the anthers; the absence of tepals; the presence of reduced or modified stipulate leaves as the bracts of the inflorescence; and the crowding out of subterminal lateral flowers through the failure of internode elongation, all suggest a relatively close relationship to the genus *Distylium*.

The complex structure of the hypanthium in *Sycopsis dunnii* and *S. laurifolia* is indicated by such anatomical features as the presence of leaf traces, independently derived from the peduncular stele, supplying the bracts on the side of the hypanthium; the presence in some flowers of secondary vascular cylinders supplying bracts and stamens on its rim; and the two complex systems of minor peripheral bundles or trunk bundle branches in its base.

The accumulated evidence suggests that the hypanthium in *S. dunnii* and *S. laurifolia* may consist of foliar, axial, and floral tissues attributable to bracts and staminate flowers of subterminal nodes, which, through condensation of the inflorescence axis, have developed upwards and fused into a tube around the naked ovary of a terminal pistillate flower. If this interpretation is correct it would appear that, as in *Distylium*, only naked unisexual flowers are present in the inflorescence, with the staminate flowers incorporated into the hypanthium around the pistillate flower, forming a bisexual pseudanthium. The hypanthium is thus neither "appendicular" nor "receptacular" (cf. discussion of these terms in Eames, 1961, p. 249, 250). It is suggestive of the syconium of *Ficus*, but differs both morphologically and anatomically (cf. Condit 1932). The term hypanthodium may be appropriate for it (see footnote 1). The ultimate fate of the hypanthium as an outgrown, ruptured structure at the base of the fruit further suggests that it is not an intrinsic part of a bisexual, perigynous flower. The exceptional behavior of *S. laurifolia* in this respect should be investigated. The vestigial peripheral bundles in the receptacles and ovaries of *S. dunnii* and *S. laurifolia*, although suggestive of the peripheral bundles in the ovary of *Distylium*, are less numerous and more localized in their origin from the receptacular stele and do not persist in the base of the ovary. Their direct contribution to the hypanthium suggests that they may represent the vestigial supply to subterminal lateral organs squeezed out in the condensation of the axis and no longer apparent morphologically, but possibly incorporated into the hypanthium. I have attempted to express this interpretation of the pseudanthium of *Sycopsis dunnii* diagrammatically in FIGURE 5s.

Sycopsis sinensis and *S. griffithiana* differ strongly from the other species of the genus in the morphology of their inflorescences and flowers, particularly in the absence of obvious reduced stipulate leaves or bract groups associated with the flowers, and the disposition of the tepals in a single cycle on the hypanthium rim. However, the two groups of species show

some similarity in their leaf form, and in the possession of urceolate hypanthia which are ruptured by the developing fruit. Anatomically, *S. sinensis* differs from *S. dunnii* in the absence of prominent secondary vascular cylinders and of the two minor bundle systems in the hypanthium. Vink's interpretation of the inflorescence bracts of *S. dunnii* would apply to *S. sinensis* only if one hypothesizes that, through a process of continued inflorescence reduction and further modification of the floral apparatus, terminal bisexual flowers such as those seen in *S. dunnii* become the axillary, sessile, apparently bisexual flowers of *S. sinensis*, with the inflorescence bracts localized in a cycle on the hypanthium rim in each flower. The irregular number and form of the tepals, the irregular number, insertion, and development of the stamens, and the irregular vascular supply to the hypanthium, perianth, and androecium might tend to support such an interpretation. But a better alternative lies in the fact that *Sycopsis sinensis* is closer morphologically to *Parrotia persica*, even though the two species differ strikingly in their leaf form, and in the degree of development of their hypanthia. The existence of morphologically intermediate first generation hybrids between them, in conjunction with the morphological and anatomical differences separating *S. sinensis* and *S. dunnii*, strongly suggests that the two groups of species in *Sycopsis* are not congeneric.

3. **Parrotia** C. A. Meyer, Verz. Pfl. Caucasus 46. 1831 FIGURES 8, 9.

A monotypic genus, containing only *Parrotia persica* (DC.) C. A. Mey., a species of small (ca. 5 m.) shrubby trees forming the characteristic arborescent component of the moist deciduous forest on the south shore of the Caspian Sea in northern Iran, where it is endemic. Its leaves are rather similar in appearance to those of *Parrotiopsis*, *Fothergilla*, and *Hamamelis*, often becoming brightly colored in the fall.

MORPHOLOGY: The inflorescence of *Parrotia* ($n = 12$, Pizzolongo 1958) consists of 2 to 8 small, inconspicuous, perfect or staminate flowers clustered in a terminal or axillary, involucrate, bracteate head. Staminate flowers, when present, are usually basal in the head, and result from reduction of the ovary. The flowers are sessile in the axils of large, broad, primary bracts (B_1 in FIGURE 8A) which are similar to the primary bracts of *Sycopsis sinensis* in their dark-brown, stellately pubescent abaxial surfaces and glabrous adaxial surfaces. The primary bracts become sharply reduced upward in the inflorescence, and secondary bracts are generally absent.

The perianth consists of a perigon of 5 to 9 (to 10, according to Endress, 1968) green tepals which are irregular in width and length, and bear long, dark-brown, silky tufted hairs at their tips. The tepals are inserted with the stamens on the rim of a shallow hypanthium. Above the hypanthium rim the tepals may be free or irregularly connate and lobed. Ten to fourteen (8 to 15) stamens are inserted irregularly on the hypanthium rim in no particular order with regard to the tepals. The stamens are similar

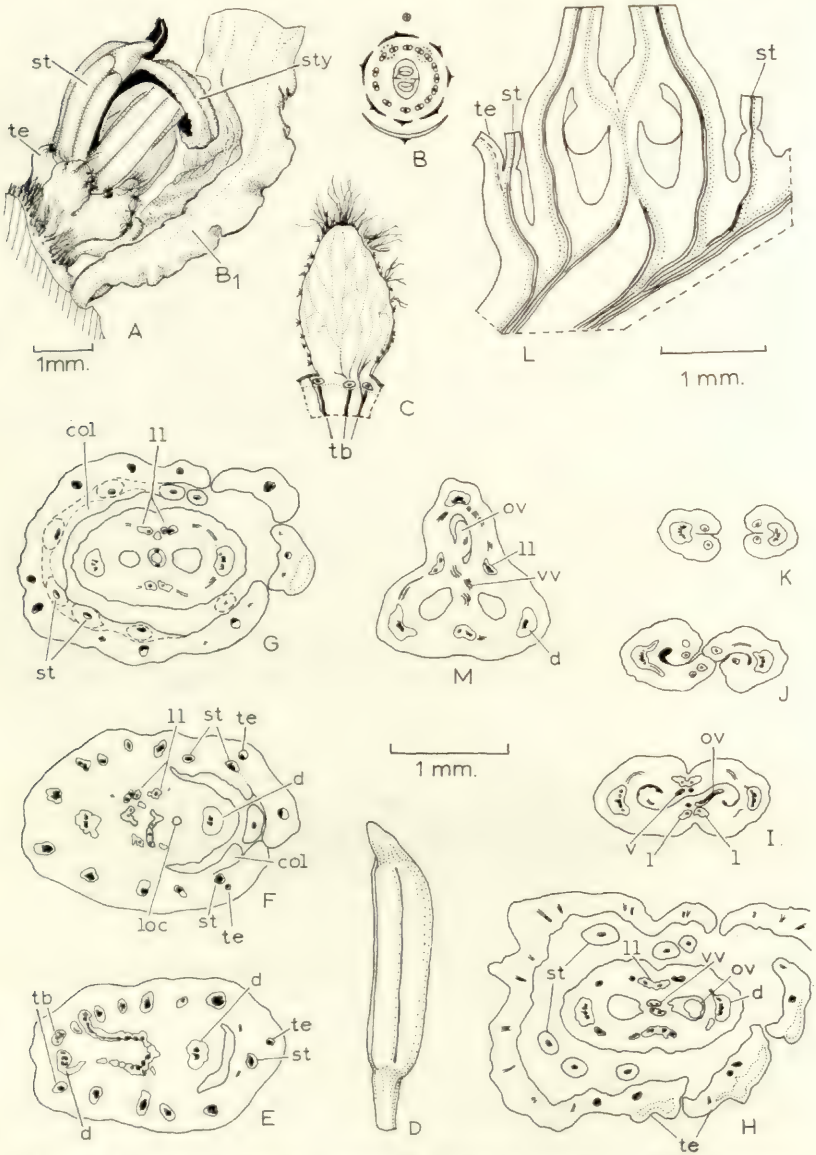

FIGURE 8. **Parrotia persica:** A, view of a flower at anthesis; B, floral diagram; C, drawing from a cleared segment of a hypanthium — note stamen scars, trunk bundles, irregular vascular supply to the tepal; D, stamen; E-K, transverse sections (slightly oblique) of a post-anthesis flower; E, through receptacle — note partially formed receptacular stele, and partial separation of the hypanthium; F, receptacle — note departing compound lateral bundles from the abbreviated receptacular stele; G, ovary near locule bases — note insertion of stamens and parenchymatous collar on hypanthium; H, mid-ovary — note perigon tube and

to those of *Sycopsis sinensis* in their strongly exserted, dark-red, linear-oblong anthers, each of which contains four pollen sacs and dehisces laterally by means of simple longitudinal slits. The anther connective is produced as a short apiculus (FIGURE 8D). On the inner edge of the hypanthium rim a number of small, vascularized, parenchymatous lobes, or a partial shallow collar, may alternate with or enclose the bases of the stamen filaments (col, FIGURE 8F, G). In the mature, non-fruiting flower the collar appears as a thickened and irregularly lobed ring of tissue on the rim, the protuberances of which suggest the abortive development of floral organs. (FIGURE 9A).

The hypanthium closely surrounds the base of a superior or nearly superior 2(–3)-carpellary ovary which is rudimentary at anthesis. The styles are long and recurved, with extensive papillate stigmatic surfaces along the length of their ventral faces.

In isolated instances tepals of *Parrotia* become quite leaf-like in appearance, with a petiole and short narrow blade (FIGURE 9A), and are similar in this respect to reduced stipulate leaves in the inflorescences of *Distylium racemosum* or *Sycopsis dunnii*. Furthermore, in a considerable number of flowers examined, particularly from the large tree in the Arnold Arboretum, but in other collections as well, aberrant carpels or bicarpellary ovaries have been observed in different positions around the functional ovary. These are inserted not on the receptacle, but on the inner face or rim of the hypanthium (FIGURE 9B, C). From 1 to 3 small ovaries of this type have been found on the hypanthium in single flowers, and in two or three flowers of the same inflorescence, occasionally developed to the point of containing rudimentary ovules. Sections of a flower containing two such ovaries are illustrated in FIGURE 9D-F, and their anatomy is briefly described below.

ANATOMY: A pedicellar stele may subtend some flowers, but is scarcely discernible beneath others in the material examined. In the latter case many of the bundles which function in supplying the hypanthium and gynoecium appear to develop almost directly from the margins of a large gap in the peduncular stele, or from a very short and longitudinally distorted cylinder of loosely arranged bundles which diverge from the gap.

In the receptacle, well below the base of the locules, 10 to 13 prominent bundles diverge from the pedicellar stele to enter the base of the hypanthium. Within the hypanthium the trunk bundles vary somewhat in the kind and numbers of organs they supply. In general, each trunk bundle divides just below the rim to supply one abaxial trace (te) to a tepal and another larger trace (st) to the base of a stamen (FIGURE 8E-G). Variations from this pattern include bundles which supply only a stamen, only a perianth lobe, or two closely set stamens and a perianth lobe. In some young flowers stamens have been found on the rim with no apparent vas-

free tepals; I, ovary, through level of ovule insertion; J, through the style bases; K, through styles; L, median longitudinal section (semidiagrammatic) through a flower; M, transverse section through a tricarpellary ovary.

cular connection through the hypanthium between the base of the filament bundle at the level of insertion and the receptacular stele. The number of traces to the base of a particular perianth lobe varies with its breadth and with the number of stamens included within the width of its base. The trunk bundles may appear collateral in transverse sections, or occasionally as narrow vascular cylinders.

In addition to the bundles described above, lateral branches from the trunk bundles, largely procambial at anthesis, were observed to move adaxially within the hypanthium to end blindly at the base of the lobes of the shallow parenchymatous collar (col) on the inner edge of the rim. The significance of these traces is uncertain, but they could indicate the abortive development of stamens in these positions.

In the ovary at anthesis only the dorsal carpel bundles are apparent, usually as protoxylem strands. The septum and ovules are scarcely, if at all, developed. In the post-anthesis ovary the dorsal bundles are prominent, and develop in close association with the hypanthial bundles (FIGURE 8E, left side). The long internode apparent between the separation of the hypanthial bundles and the carpel dorsal bundles from the receptacular stele in *Sycopsis sinensis* is absent in the receptacle of *Parrotia persica*.

The compound lateral bundles (ll) originate from the receptacular stele in the transverse plane well above the departing dorsal bundles, and ascend as multi-stranded vascular bands at each edge of the septum. The central bundles in each band consolidate into a broad vascular arc in the upper half of the ovary. In polarized light two distinct protoxylem strands are apparent in each arc, indicating two adjacent lateral bundles. The individual lateral bundles separate at about the level of ovule insertion (FIGURE 8F-I).

Above the departure of the compound laterals the remaining portions of the receptacular stele consolidate to form a narrow and largely procambial cylinder. At about mid-height in the septum the cylinder divides in the median plane to form two largely procambial compound ventral bundles (vv, FIGURE 8H, M). The latter divide transversely just below the level of ovule insertion, and the individual ventral bundles shortly supply traces to the ovules, then fuse with the adjacent lateral bundles and pass upward as the marginal bundles of the styles (FIGURE 8H-K).

In the base of some ovaries examined a few small procambial bundles occur which are similar to the peripheral bundles in the base of the ovary of *Distylium*. They originate from the receptacular stele well above the departure of the hypanthial bundles and mainly in the vicinity or even from the base of the departing compound laterals. They are deflexed, and appear to end blindly near the periphery of the ovary base, near or just below the level of separation of the hypanthium from the ovary. Occasionally branches from such a bundle can be traced into and upward in the hypanthium, where they end blindly in or near the parenchymatous collar, and upward in the ovary wall above the level of their separation from the stele.

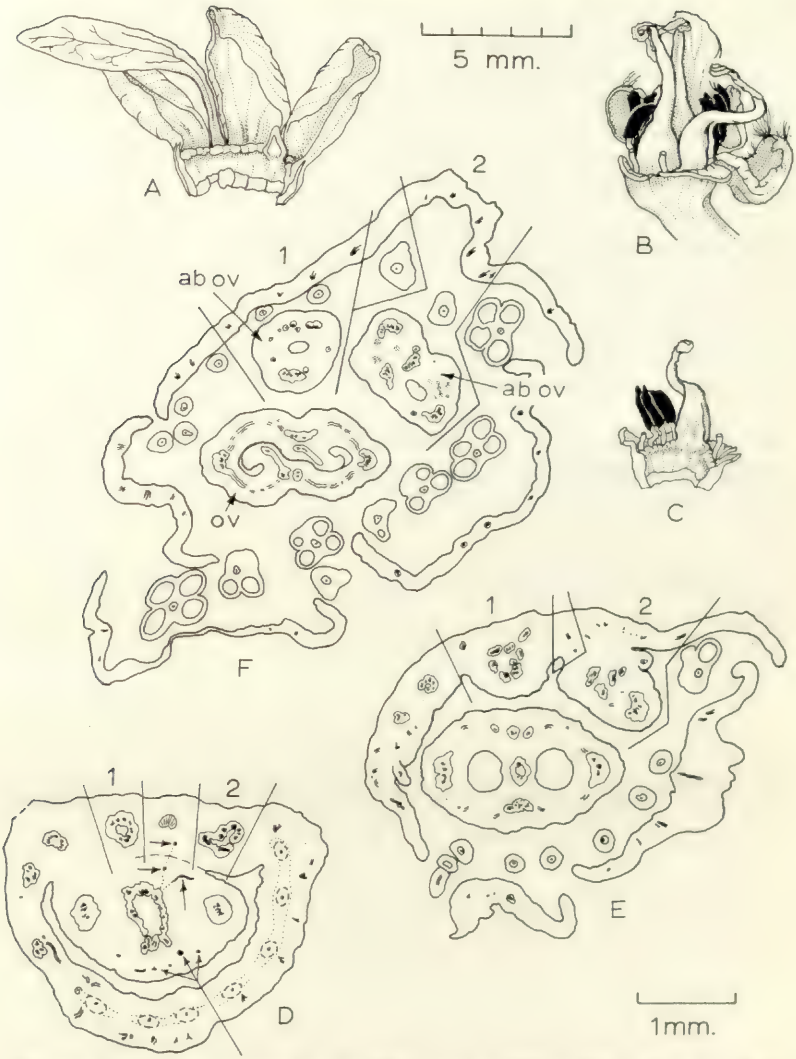

FIGURE 9. **Parrotia persica:** A, leaf-like tepal on hypanthium rim; B, whole flower, near tepals excised — note the single carpel (right) on the hypanthium, with suture directed outward; C, section of hypanthium from B, bearing the carpel; D-F, transverse sections through a flower bearing two anomalous ovaries on the hypanthium (slightly oblique); D, through base of functional ovary and hypanthium (above) — note the two steles in the hypanthium; E, ovaries and abaxial stamens and tepals forming on the hypanthium; F, areas of perianth and androecium supplied by each stele indicated as zones 1 & 2.

In those flowers containing anomalous ovaries on the hypanthium rim, anatomical study shows that a substantial vascular cylinder is pinched

off from the pedicellar stele and enters the hypanthium beneath each ovary. Most of the bundles in each cylinder are used up in supplying the ovary, but tepals and stamens adjacent and abaxial to the ovary on the rim also receive their traces from the cylinder. In FIGURE 9D-F the sectors (1 and 2) of the perigon and androecium supplied by two such steles are indicated. However, no regular pattern of insertion and vascular supply of tepals and stamens relative to the anomalous ovaries was apparent.

The morphological resemblances between *Parrotia persica* and *Sycopsis sinensis* are striking, and the description of the intergeneric hybrid × *Sycoparrotia* confirms their close affinity. They are very similar in their capitate inflorescences; in the form and pubescence of the primary inflorescence bracts; in the pubescence, variable number, and extremely irregular form of their tepals; in the irregular number and insertion of the stamens, and the similar form, dehiscence, and reddish color of their anthers; in their essentially superior ovaries; and in the irregular vascular supply to the hypanthium and its attendant organs.

In *Parrotia persica* the number of tepals (5 to 10) and stamens (8 to 15) is usually greater, and the tepals considerably longer and broader, than in *Sycopsis sinensis*, which has 4 to 7 tepals and 5 to 10 stamens. In *S. sinensis* the hypanthium is longer, and the basal connation of its tepals into a perigon tube above the hypanthium rim is more pronounced than in *Parrotia persica*. In fruit the shallow hypanthium of *Parrotia* is not ruptured, as in *Sycopsis sinensis*.

But *Parrotia* exhibits certain morphological and anatomical features in common with *Distylium*, and to a limited extent with *Sycopsis dunnii*. The tepals of *Parrotia*, in particular, suggest varying manifestations of the reduced stipulate leaves which form the inflorescence bracts and "perianth" in the pseudanthia of *Distylium racemosum*, *D. gracile*, and *D. buxifolium*. The occasional presence of a reduced but obvious leaf blade among the tepals of *Parrotia* enhances this interpretation of their morphological nature.

Also striking in *Parrotia* is the presence in the receptacles of some flowers of peripheral bundles which supply branches both to the base of the ovary and the base of the hypanthium, as in *Sycopsis dunnii*. These are similar in origin and appearance to those of *Distylium*, but not as numerous or as strong.

On the basis of the available evidence it appears possible that the flower of *Parrotia persica* may represent a pseudanthium of a more advanced type than that seen in *Distylium*, developed through the complete reduction of an inflorescence axis, and resulting in the aggregation of reduced stipulate leaves (bracts) of subterminal nodes, and modified naked staminate flowers of suppressed lateral axes, around the functional ovary of the naked terminal pistillate flower. I have observed terminal and lateral pseudanthia approaching this level of reduction in some relatively reduced inflorescences of *D. gracile* and *D. buxifolium*. The union and elevation of the bracts and modified staminate flowers on the shallow

hypanthium may explain the variability in the number of bundles supplying the base of the hypanthium, and the variability in their form. The peripheral bundles of the receptacle may be attributable to suppressed lateral organs of the condensed inflorescence axis, and the appearance of abortive carpels or ovaries on the hypanthium in otherwise normal flowers may be due to the aberrant development of pistils attributable to the terminal ovaries of lateral axes which are usually suppressed in the pseudanthium. The occurrence of these anomalous ovaries, and leaf-like bracts, on the hypanthium is certainly teratological, and of only secondary importance as evidence. But such organs have not been observed on hypanthia in any other genus of the family, and should not be ignored.

The interfertility of *Parrotia persica* and *Sycopsis sinensis* indicates that they are relatively recent derivatives of a common ancestral stock. If the above interpretation of the *Parrotia* flower is correct, then the longer hypanthium of *Sycopsis sinensis* may represent only an elaboration in length of a shorter ancestral hypanthium, perhaps as in *Parrotia*, with concomitant reduction in the number of bracts and stamens inserted on the rim of its narrower throat, and in increased basal connation of the tepals above the rim.

4. **Fothergilla** J. A. Murray, Syst. Veg. ed. 13. 418. 1774. FIGURE 10.

The genus *Fothergilla* consists of two species of low deciduous shrubs which usually reach a height of 1 to 3 meters and frequently form dense clumps through rhizomatous proliferation (Ernst 1963; Weaver 1969). The species are limited in distribution to the coastal plains and uplands of the southeastern United States.

MORPHOLOGY: The inflorescence of *Fothergilla* contains numerous sessile flowers solitary in the axils of broad primary bracts spirally arranged in a terminal spike (FIGURE 10A). The flowers are incomplete, perigynous, and generally bisexual, although a few basal flowers in the inflorescence may be functionally staminate, containing only a rudimentary ovary. The perigon and androecium are inserted on a shallow, campanulate hypanthium which surrounds the ovary and is fused with it for its lower third. The perianth consists of 5 to 7 (–8) small, irregular tepal lobes (te) of variable size and position (FIGURE 10A, I-K). I found 18 to 24 stamens in flowers of *Fothergilla gardenii* (n = 24, Weaver 1969), and up to 31 stamens in those of *F. major* (n = 36, Weaver 1969; Weaver found 12 to 24 stamens in *F. gardenii*, and 22 to 32 in *F. major*), inserted in a single cycle on the rim of the hypanthium with their bases enclosed externally by the lobes of the perigon and internally by a shallow, much lobed inner parenchymatous lip (col) of the hypanthium (FIGURE 10I-K). The distally clavate, unequal filaments are several times longer than the hypanthium, and bear small, basifixed anthers which contain four pollen sacs. Anther dehiscence is subvalvate and lateral by means of longitudinal I-shaped slits (FIGURE 10C). There are no staminodia. The ovary is up to one-fourth semi-inferior. The two carpels terminate in filiform styles with inconspicuous

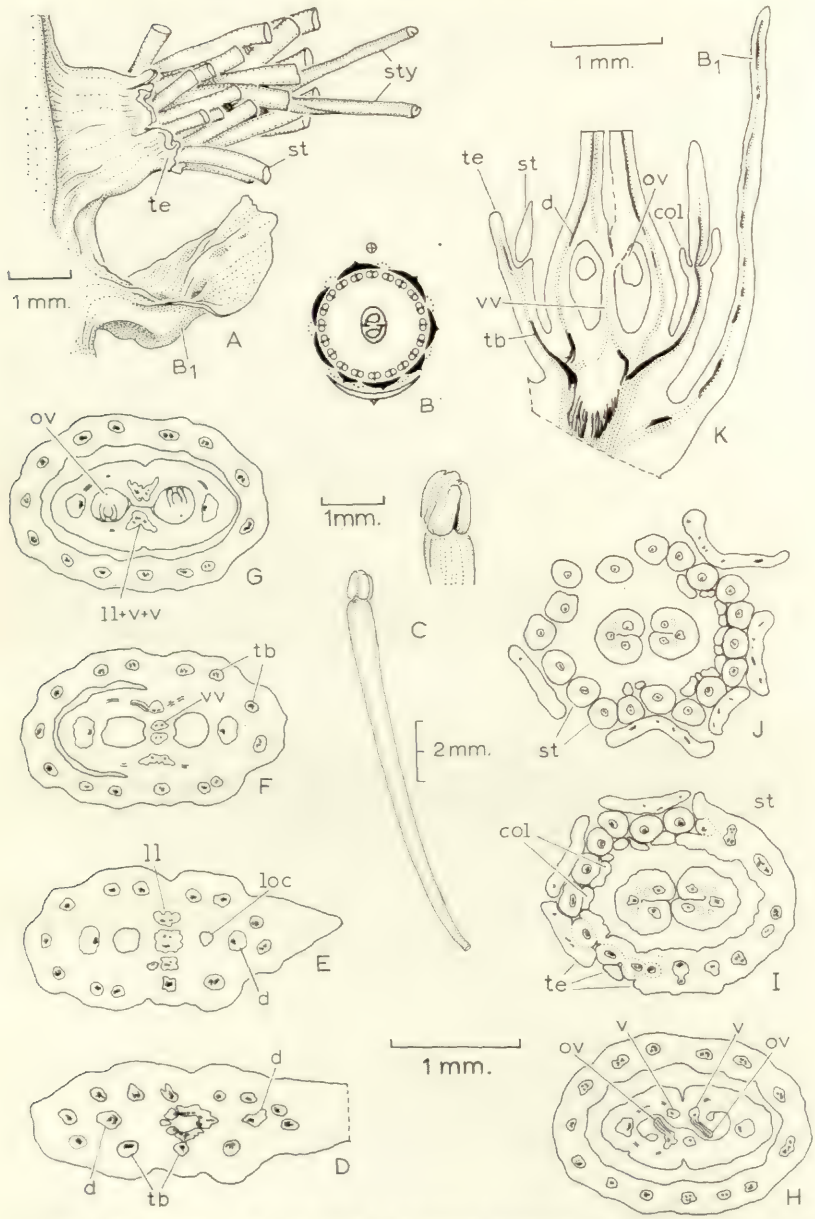

FIGURE 10. **Fothergilla gardenii:** A, a flower at anthesis, stamens and styles cut away; B, floral diagram; C, stamen; D-J, transverse sections through a flower at anthesis; D, through receptacle — note dorsal bundles and receptacular stele; E, bases of the locules — note compound lateral bundles and residual receptacular stele; F, partial separation of the hypanthium, compound ventral bundles formed;

papillate stigmas within the folded margins of the distal half. Each locule contains one or occasionally two ovules, the lower of which is fertile.

ANATOMY: The vascular supply to the base of each flower varies from a short but cylindrical pedicellar stele to a reduced condition in which a variable number of large bundles enter the receptacle directly from the margins of an elongate gap in the peduncular stele.

In the receptacle, well below the base of the locules, several large trunk bundles (tb) diverge from the pedicellar stele to enter the base of the hypanthium, eventually to supply the perianth and androecium. An internode is not present in the receptacular stele between the trunk bundles and the carpel dorsal bundles, and the latter are formed at either side of the receptacle in the median plane by the fusion of 2 to 3 lateral branches from single or adjacent trunk bundles (d in FIGURE 10D, E). Above the departure of the associated trunk and dorsal bundles the remaining bundles of the receptacular stele converge on the center of the receptacle to form a narrower receptacular cylinder (FIGURE 10D) which then shortly gives rise to two compound lateral bundles (ll) to either side in the transverse plane. The remaining traces in the stele consolidate to form a still narrower and largely procambial cylinder which enters the base of the septum. In polarized light at least two strands of protoxylem appear in this cylinder, situated on opposite sides in the tranverse plane (FIGURE 10E).

The number of bundles entering the base of the hypanthium approximates half the number of stamens eventually supplied, but there is no exact correlation in this respect. Within the hypanthium the number of trunk bundles is increased by branching. Rarely, lateral branches from adjacent bundles fuse to form a single trunk bundle. More often, minor lateral branches of the trunk bundles end blindly in the hypanthium slightly below the level of stamen insertion.

Each stamen receives a single trace. A single trunk bundle may supply only one stamen, but many of the trunk bundles branch immediately below the insertion of the stamens to form 2 to 3 stamen traces. In addition, almost every trunk bundle produces a single, relatively minor trace (te) at this level, which enters the base of a tepal. Occasionally a relatively weak hypanthial bundle will supply only a tepal. There was no apparent regularity in the vascular supply to the tepals. Within the tepal the traces may branch, and anastomoses may form between adjacent branches.

In the ovary the division of the compound ventral (vv) and compound lateral (ll) bundles to form distinct ventrals and laterals usually occurs slightly below the level of ovule insertion, as figured by Horne (1914), but occasionally the compound laterals were observed to divide in the lower half of the ovary, or to remain entire to a level slightly above ovule insertion. The free ventral and lateral bundles of each margin then fuse,

G, ovary — note fusion of compound lateral and compound ventral bundles; H, ovule insertion; I, insertion of the stamens on the hypanthium; J, through the various organs of the flower; K, nearly median longitudinal hand section (semi-diagrammatic) of a flower at anthesis.

and immediately above the point of fusion an ovular trace separates from the ventral bundle of each fertile margin and enters the funiculus of the ovule (FIGURE 10H).

At anthesis the upper portions of the ventral bundles are frequently in only a procambial condition, and in some carpels the ventral bundle to the sterile margin appears to die out soon after separating from the adjacent ventral which supplies the fertile margin.

Fothergilla, one of the better known genera of Hamamelidoideae, is widespread in cultivation and easily accessible for study. Baillon (1871) described the organogeny of *Fothergilla alnifolia* L. (= *F. gardenii* Murr.). According to his observations 5 to 7 short sepal primordia develop successively on the rim of a shallow, cupulate receptacle. The first and second primordia appear on either side, then the others develop in the intervals between the first two. Later, one stamen primordium develops before each small sepal, then 2, 3, or 4 stamen primordia appear secondarily on the sides of each initial stamen. Baillon considered the smaller, secondary stamen primordia opposite each calyx lobe to be exterior to the primary stamen initial, and interpreted the groups of stamens as having arisen through the divisions of a primitive stamen opposite each sepal. He did not interpret his observations in terms of cycles of stamens.

Tong (1930), however, states that the normal number of stamens is 14 in *Fothergilla major*, arranged in two whorls, the outer of which alternates with the calyx lobes. He considered the outer whorl of stamens derived through the transformation of petals to stamens, a view which he attributes justifiably also to DeCandolle (1830), and Griffith (1838). Excess stamens were interpreted as being derived through splitting of stamen primordia. Tong's floral diagram accordingly shows the stamens arranged in two cycles.

Shoemaker (1905) observed some stages of the organogeny and embryology of *Fothergilla gardenii*. His observations on the development of the stamens agree with those of Baillon. Flint (1957) has provided a detailed description of megasporogenesis and megagametogenesis in both *Fothergilla gardenii* and *F. major*.

Horne (1914) illustrated his brief description of the floral vasculature of *Fothergilla major* with three drawings of transverse sections at critical levels. My observations on *Fothergilla* are in general agreement with those of Horne.

There is a slight difference in the relative positioning of the stamens on the rim of the hypanthium, so that the stamen opposite the mid-line of each tepal appears slightly adaxial to its neighbors. This is especially apparent in those flowers having more numerous stamens (*Fothergilla major*), but it is not sufficiently pronounced either morphologically or anatomically to provide a basis for recognizing more than one cycle of stamens on the hypanthium.

The lobed collar on the inner edge of the hypanthium rim of *Fothergilla* is similar to that seen in *Parrotia persica*, but there is no vascular supply

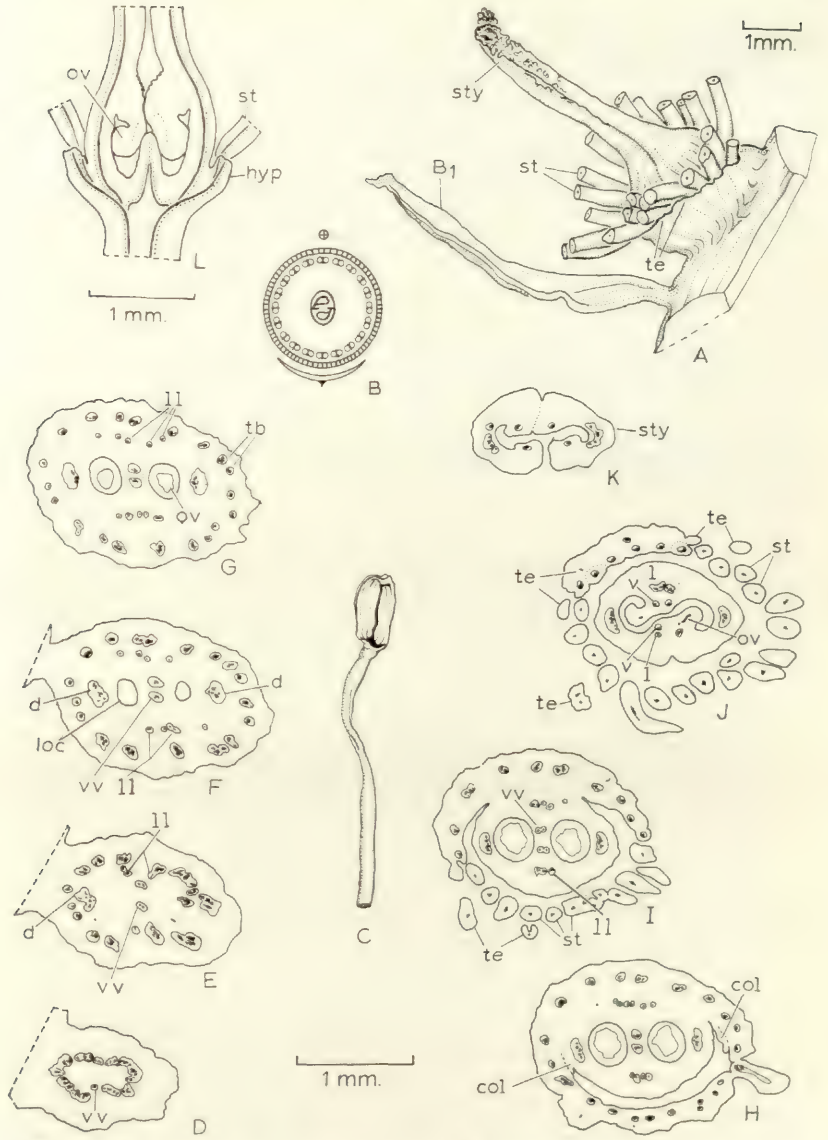

FIGURE 11. **Parrotiopsis jacquemontiana:** A, flower at anthesis, stamens cut away; B, floral diagram; C, stamen; D–K, transverse sections through a flower at anthesis; D, pedicellar stele; E, through the receptacle — note gynoecial bundles differentiating; F, bases of the locules; G, ovary — note diffuse compound lateral bundle traces; H, partial separation of the hypanthium, compound lateral bundle traces consolidating; I, ovary — note individual ventral bundles forming; J, ovule insertion; K, through the style bases; L, median longitudinal hand-section (semidiagrammatic) of a flower at anthesis.

evident to its base. Nor is there any evidence in the receptacle of peripheral bundles or vestigial vasculature of any kind. The loss of an internode in the receptacular stele, resulting in the close association or partial fusion of the carpel dorsal bundles with the hypanthial trunk bundles, is also seen in *Parrotia*, but in both genera a segment of the receptacular stele intervenes below the departure of the compound lateral bundles, and continues upward into the base of the septum. The origin of the ovular traces above the fusion of the lateral and ventral bundles is a deviation from their departure prior to fusion in *Distylium*, *Sycopsis*, and *Parrotia*.

5. **Parrotiopsis** (Niedenzu) Schneider, Handb. Laubholzk. 1: 429. 1905. FIGURE 11.

This monotypic Asian genus of deciduous shrubs or small trees is known only through the species *Parrotiopsis jacquemontiana* (Decne.) Rehd., which has a restricted distribution in the Himalayan mountains of northern Kashmir, West Pakistan, and Afghanistan (see Kammeyer 1957, p. 73, for distribution map).

MORPHOLOGY: The inflorescence of *Parrotiopsis* ($n = 12$, Anderson & Sax 1935) contains about a dozen small, inconspicuous flowers arranged in a terminal subcapitate spike. The blades and stipules of the leaves at the two or three lowest nodes of the inflorescence are conspicuously expanded into spreading white bracts which form a showy involucre around the flowers. A single sessile flower, usually staminate through reduction of the ovary, is axillary to each set of involucral bracts. Primary bracts may subtend a few flowers just above the involucre, but are absent at the distal nodes of the inflorescence, and secondary bracts were not present in the material examined.

The flowers are regular, apetalous, perigynous, and usually bisexual, with a semi-inferior ovary (FIGURE 11H, L). The perianth and androecium are inserted on the rim of a shallow, cupulate hypanthium which is fused basally with approximately the lower third of the ovary, while the free portion of the hypanthium forms a shallow cup around the middle of the ovary. The limb of the perianth is reduced to irregular lobes on the margin of the hypanthium. Occasionally one or two tiny, pubescent tepals, less than 1 mm. long, develop. About 21 to 25 stamens with unequal, terete filaments, are inserted in a single cycle on the rim of the hypanthium. The small, oblong, truncate anthers contain four pollen sacs and dehisce laterally by means of four valves (FIGURE 11C). The anther connective may be produced as a very short apiculus on the adaxial edge of the truncate tip. A very shallow, thin, parenchymatous collar on the inner edge of the hypanthium encloses the stamen filament bases. In the ovary one or occasionally two ovules are found in each locule. The styles are linear, with papillate stigmas running nearly the entire length of the ventral margins.

ANATOMY: A cylindrical pedicellar stele is present beneath each flower. In the receptacle the stele expands as 13 to 19 trunk bundles differentiate

and diverge toward the periphery to enter the base of the hypanthium (FIGURE 11D-H). Adnation between the bundles of the hypanthium and gynoecium in *Parrotiopsis* is relatively advanced over that in *Parrotia* and *Fothergilla*, as evidenced by the fact that there is no indication of a vascular cylinder in the receptacle.

The 13 to 19 trunk bundles (tb) which enter the base of the hypanthium eventually supply 21 to 25 stamens, as well as the tepals. As in *Fothergilla*, each stamen receives a single trace (st) from a trunk bundle, and some trunk bundles divide within the hypanthium to form additional bundles, or divide just below the insertion of the stamens to form two or three stamen traces (FIGURE 11F-I).

The limb of the perianth is so reduced that few of the lobes were vascularized in the material which I examined. The few traces (te) produced by the trunk bundles to the tepal lobes are very inconspicuous at anthesis. This is in contrast with *Fothergilla*, in which almost every one of the numerous trunk bundles produces a single abaxial branch to the perianth. Because of this reduced condition I am unable to confirm Saunder's observation (1939) that the stamens are supplied from both the midveins and lateral veins of the calyx lobes.

In the receptacle the gynoecial bundles appear to have independent origins in the fusions of branches from the bundles of the expanding pedicellar stele, rather than arising from a cylindrical receptacular stele. At either side of the receptacle in the median plane 3 to 4 small branches from diverging trunk bundles converge and fuse to form a carpel dorsal bundle (d, FIGURE 11E, F). In the transverse plane 4 to 6 traces converge centripetally to function in the formation of the compound ventral (vv) and compound lateral bundles (ll). The compound ventrals are often the first to differentiate, in some flowers appearing as a single bundle on each side of the receptacle (FIGURE 11C, E), while the comopund laterals form at a slightly higher level as an aggregation of 4 to 5 weak bundles arranged in a loose band at each edge of the septum (FIGURE 11F, G).

In the ovary the several bundles of each compound lateral consolidate distally to form a narrower band, or a single broad bundle which dichotomizes at about the level of ovule insertion to form the independent lateral bundles (l). The compound ventrals divide above the middle of the ovary, forming four ventral bundles (v) which fuse with the adjacent laterals at the level of ovule insertion. Ovular traces (ov) depart from the ventrals of the fertile margins just prior to this fusion (FIGURE 11H-J).

The genus *Parrotiopsis*, like *Fothergilla*, is also widespread in cultivation, and has been studied by several workers. Horne (1914) included two figures of transverse sections illustrating the basic vascular pattern of the ovary (as *Parrotia jacquemontiana*), and in one of these two ovules are conspicuous in each locule. Tong (1930) interpreted the stamens of *Parrotiopsis* as forming three alternating septenate cycles within a cycle of seven calyx lobes. Saunders (1939) described the origin of the stamen traces as being "detached from the sepal lateral veins as well as from

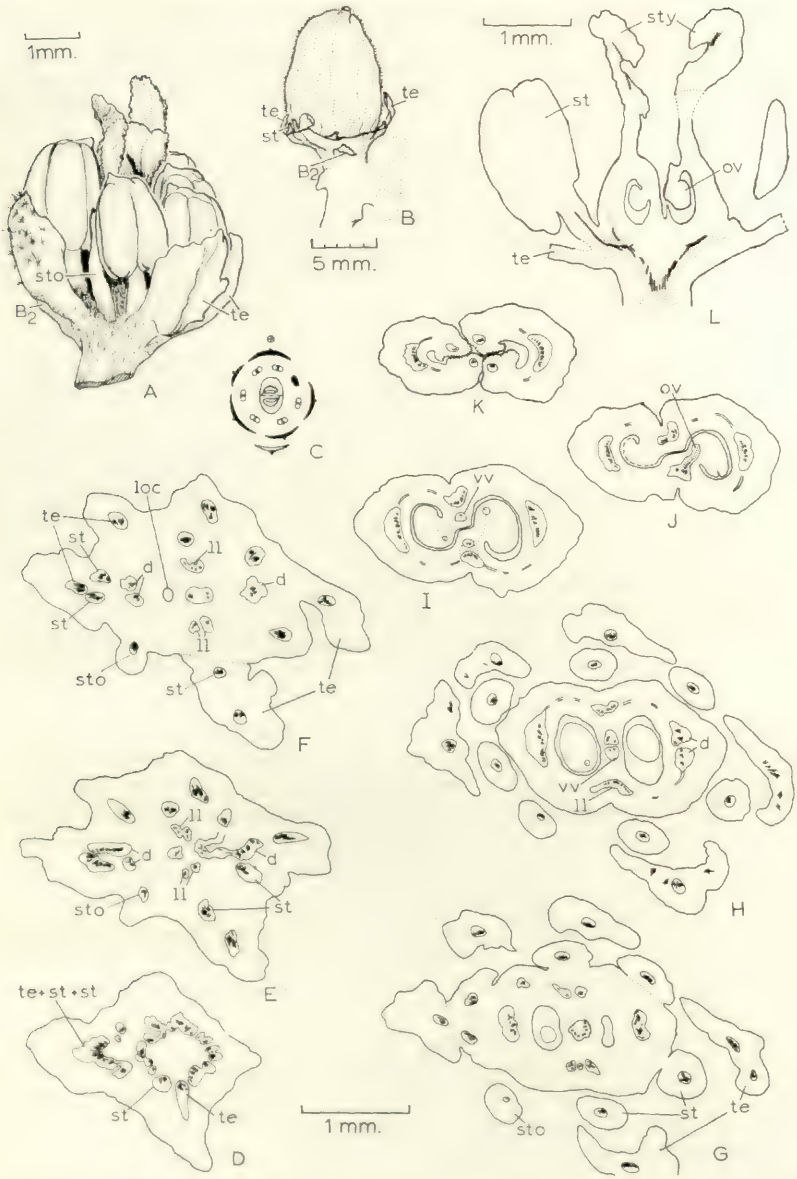

FIGURE 12. **Molinadendron sinaloense:** A, view of a flower at anthesis; B, nearly mature fruit — note shallow hypanthium; C, floral diagram; D-K, transverse sections of a flower at anthesis (slightly oblique); D, through the receptacle, some tepal and stamen traces forming; E, receptacle, gynoecial bundles forming (d, ll); F, bases of the locules, insertion of some tepals and stamens; G, stamens separating from base of the ovary; H, about mid-height in the ovary; I, base of ovule insertion; J, top of ovule insertion; K, through the style bases; L,

the midrib bundles and [standing] in a single ring." Kaul (1969) found that the endosperm is *ab initio* cellular in *Parrotiopsis*.

The systematic affinities of the genus are indicated by the fact that at one time or another, *Parrotiopsis jacquemontiana* has been included in both *Fothergilla* (Niedenzu 1891) and *Parrotia* (Decaisne 1844), as well as by Rehder's statement (1920) that *Parrotiopsis* differs from *Fothergilla* "only in the capitate inflorescence supported at the base by large bracts, [and] in the less numerous stamens with linear not club-shaped filaments . . .", a view expressed earlier by Hooker (1896). However, *Parrotiopsis* is more advanced than *Fothergilla* in its fewer-flowered, more congested inflorescences, in the extreme reduction of its perianth, and in the slightly more pronounced adnation between hypanthium and ovary. It is also more advanced anatomically in the absence of a residual receptacular cylinder, resulting in basal adnation between the hypanthial and gynoecial vascular systems. The diffuse origin of the compound lateral bundles, and the individuality of the compound ventrals in the receptacle, are apparently artifacts of the reduction of the receptacular stele and the greater adnation between hypanthium and ovary. I could find no morphological or anatomical basis for assigning stamens to more than one cycle on the hypanthium.

6. **Molinadendron** Endress, Bot. Jahrb. **89**: 353. 1969. FIGURE 12.

The genus *Molinadendron* is a small Central American group recently segregated from *Distylium* Sieb. & Zucc. (cf. Harms 1933; Walker 1944; Gentry 1948; Balgooy 1966). The genus contains three as yet little known species of large evergreen trees. *Molinadendron guatemalense* (Radlk. ex Harms) Endress is apparently restricted to the vicinity of Coban, Guatemala. *Molinadendron hondurense* (Standl. in Walker) Endress occurs widely in Honduras, while *M. sinaloense* (Standl. & Gentry) Endress is restricted to the mountains of the State of Sinaloa, Mexico. The following descriptions are based primarily on material of *M. sinaloense* which I collected in 1964. In addition, flowers from herbarium sheets of the other two species were also examined anatomically, and showed no significant difference from those of *M. sinaloense*.

MORPHOLOGY: The inflorescences of *Molinadendron sinaloense* are axillary or terminal on short lateral leaf-bearing shoots of the current season's growth. Each consists of about a dozen small inconspicuous flowers spirally arranged in a short, congested spike. The proximal flower may be axillary to a much reduced stipulate leaf, the blade of which may be little more than a narrowly triangular bract. Intermediate flowers in the inflorescence are subtended by obvious primary bracts which are more or less hooded and cover the flower in bud; but at distal nodes the primary bracts are reduced and adnate to the base of the flower, often intergrading with the tepals of the perigon. Similarly, a pair of subopposite secondary

longitudinal section through a post-anthesis ovary, rather oblique — note slightly perigynous insertion of stamens.

bracts may subtend the lowest flower or two, but at higher nodes these either fail to develop, or are adnate to the floral receptacle and indistinguishable from the tepals. It is often easier to fix the presence and position of these bracts in the elongated, more open fruiting inflorescence than at anthesis.

The flowers at anthesis are sessile or nearly so, incomplete, subperigynous, and bisexual. The perianth consists of 2 to 8 linear to broadly cuneate-dentate and sometimes cucullate tepals (or fewer if some of these are secondary bracts). Petals are absent. Two to eight (usually 5 to 7) bright-red stamens are arranged in a single cycle around the base of the sessile, broad-based ovary. The anthers, which are short-oblong with a truncate apex and a short adaxial apiculus, are borne on short terete filaments which elongate after anthesis. Each anther contains four pollen sacs, and dehisces laterally by means of four narrow, longitudinal valves. The two- (occasionally three-) carpellary ovary appears superior but is slightly sunken in the broad receptacle, and hence slightly inferior. It is incompletely bilocular, and contains one or sometimes two (then one on each margin) ovules in each locule. The placentation is parietal in my material, rather than axial as described by Endress (1969) (cf. FIGURE 12I). The styles are exserted, recurved, and somewhat expanded distally, with extensive papillate stigmatic surfaces.

The basal flower(s) and sometimes the terminal flower in an inflorescence may be staminate through reduction of the ovary. Abortive stamens, reduced in varying degrees to subulate sterile filaments (sto in FIGURE 12A), and abortive linear, bristle- or scale-like, pubescent perianth bracts frequently appear in any part of the inflorescence. A striking feature of the flowers is the irregularity in number and insertion of the tepals and stamens. There appears to be a rough correlation between the number of stamens and the number of tepals in the perianth. They are often equal, with a stamen opposite each tepal, but frequently the number of stamens is larger, and their insertion irregular. And in some flowers the stamens alternate with the tepals. In fruit the marcescent tepals and stamens, or their basal portions, are prominent on the rim of the very shallow hypanthium around the base of the nearly superior bony capsule (FIGURE 12B).

ANATOMY: In the pedicel a short cylindrical stele assumes an elliptic configuration as its vascular strands become organized into traces to the floral organs. Each tepal (te) receives a single trace, as does each stamen (st). Opposing tepals and stamens frequently receive their traces from a common trunk bundle in the receptacle, but this is not a constant feature, since, in some cases, each may be supplied by a trace derived independently from the stele. Alternating tepals and stamens each receive independent traces from the stele. When two stamens oppose a single tepal each stamen is supplied by an independent stamen trace, rather than by branches of a single stamen or tepal trunk bundle. In transverse sections the adnation of the perianth and androecium to the base of the ovary is evident (FIGURE 12F, G).

In the receptacle, the carpel dorsal bundles may be fused basally for a short distance with some of the traces supplying the perianth and androecium as a result of the loss of an intervening internode in the receptacular stele. However, a short segment of the stele persists above the departure of these traces, giving rise to the compound lateral and compound ventral bundles.

At the median sides of the expanding receptacular stele, 2 to 3 small vascular strands from diverging tepal or stamen bundles move centripetally to associate or fuse into a dorsal bundle (d in FIGURE 12E, F). In the base of the ovary a dorsal bundle may be entire (FIGURE 12E, right side) or consist of two large collateral bundles which then fuse at a higher level into a single broad bundle (FIGURE 12E-G, left side).

Above the departure of the sepal, stamen, and dorsal bundle traces the residual bundles of the receptacular stele move toward the center of the receptacle. In the plane of the septum 1 to 3 of these on each side cease their centripetal movement and assume a position about midway between the periphery and the center. These form the compound lateral bundles (ll) at each edge of the septum. The remaining residual bundles converge and form a narrow cylinder in the base of the septum (FIGURE 12E, F).

A compound lateral may appear as a single broad bundle in the base of the ovary, or as a group of 2 to 3 vascular strands which fuse above into a common compound bundle (FIGURE 12E-H). The compound laterals usually dichotomize transversely at the level of ovule insertion or slightly above.

The narrow residual receptacular cylinder divides about midway up the septum to form two compound ventral bundles (vv), each containing 1 to 3 strands of protoxylem, which diverge toward the edges of the septum.

At anthesis the compound ventrals and laterals may vary in form in the upper part of the septum and parietal placentae. Usually each dichotomizes in the transverse plane at about the level of ovule insertion to form individual ventral and lateral bundles which then fuse in pairs and pass into the styles as marginal bundles. In this case the ovular trace originates from an individual ventral bundle prior to its fusion with the adjacent lateral. Sometimes, however, the compound ventral and lateral bundles fail to divide, but fuse in the placenta, and the bundle thus formed then dichotomizes at a slightly higher level to form the marginal bundles of the styles. In this case the ovular trace may originate from the compound ventral either below or above its fusion with the compound lateral. Exceptionally a compound ventral bundle will pass into the funiculus of the ovule without dividing, with no discernible connection to the adjacent compound lateral bundle. The latter condition may be due to the immature state of the ovary and its vasculature at anthesis, or it may represent a form of reduction in the vascular pattern of the ovary concomitant with reduced size. It has been noted in other genera of the family as well.

The flowers of *Molinadendron* differ from those of *Distylium* in their spicate arrangement; in the presence of a perianth; in their bisexual condition (or occasionally staminate through reduction of the ovary);

in the valvate dehiscence of the anthers; in the slightly inferior condition of the ovary, and in the persistence of the sepals and stamens on the rim of a very shallow hypanthium around the base of the fruit (FIGURE 12B. See also Gentry 1948, *figure 1*). Anatomically, the vestigial peripheral bundles of the *Distylium* ovary are absent, the carpel dorsal bundles are fused basally with the tepal and stamen traces, and fusion of adjacent lateral and ventral bundles in the septum and placentae tends to be more advanced.

Perhaps the most striking feature of the flowers is the irregularity in the numbers and insertion of the tepals and stamens, and the intergradation of the primary and secondary bracts with the tepals. One is frequently at a loss to know which is which. Endress (1969) concluded that "*Molinadendron* does not even belong to the tribe Distylieae (*Distylium*, *Sycopsis*, *Matudaea*), but shows more relationship to *Fothergilla*/*Parrotiopsis* and *Fortunearia*/*Sinowilsonia*." However, the pollen morphology of *Molinadendron* differs markedly in the form of its exine reticulum, and in the shape and sculpturing of its apertures (Chang 1960, Bogle, unpublished scanning electron micrographs), from that of *Fothergilla* and *Parrotiopsis*, and is closer to that of *Sinowilsonia* and *Distylium*. The distinct one-trace tepals of *Molinadendron* also differ from the irregularly vascularized tepals of *Fothergilla*.

The genus *Fortunearia* differs from *Molinadendron* most strikingly in its regular, complete, usually pentamerous flowers, as well as in its numerous-flowered racemose inflorescences, subvalvate anther dehiscence, and half-inferior ovaries. Each sepal in *Fortunearia* receives one median and two lateral traces. In *Sinowilsonia*, unisexual flowers and inflorescences are well developed, and the flowers are racemosely arranged, regular, more or less complete, and usually pentamerous, with an urceolate hypanthium surrounding the superior ovary in the pistillate flowers. Stamen dehiscence in the staminate flowers is subvalvate, by means of I-shaped slits, as in *Fortunearia*.

These morphological differences, in conjunction with its New World distribution, suggest that *Molinadendron* occupies a relatively isolated position among the apetalous Hamamelidoideae.

7. **Matudaea** Lundell, Lloydia 3: 209. 1940 FIGURE 13.

The genus *Matudaea* consists of only two poorly defined species of large, possibly evergreen trees distributed in Mexico and Central America. *Matudaea trinervia* is known from a few scattered locations in Honduras, Guatemala (Standley & Steyermark 1946), and the State of Chiapas, Mexico. *Matudaea hirsuta* Lundell (1961) is known only from a small area in the southern part of the State of Mexico, and differs from *M. trinervia* principally in its densely hirsute twigs. Specimens more or less intermediate between these two species have been collected in the State of Jalisco, Mexico, by McVaugh *et al.* (personal communication).

The following descriptions are based primarily on flowers of *Matudaea*

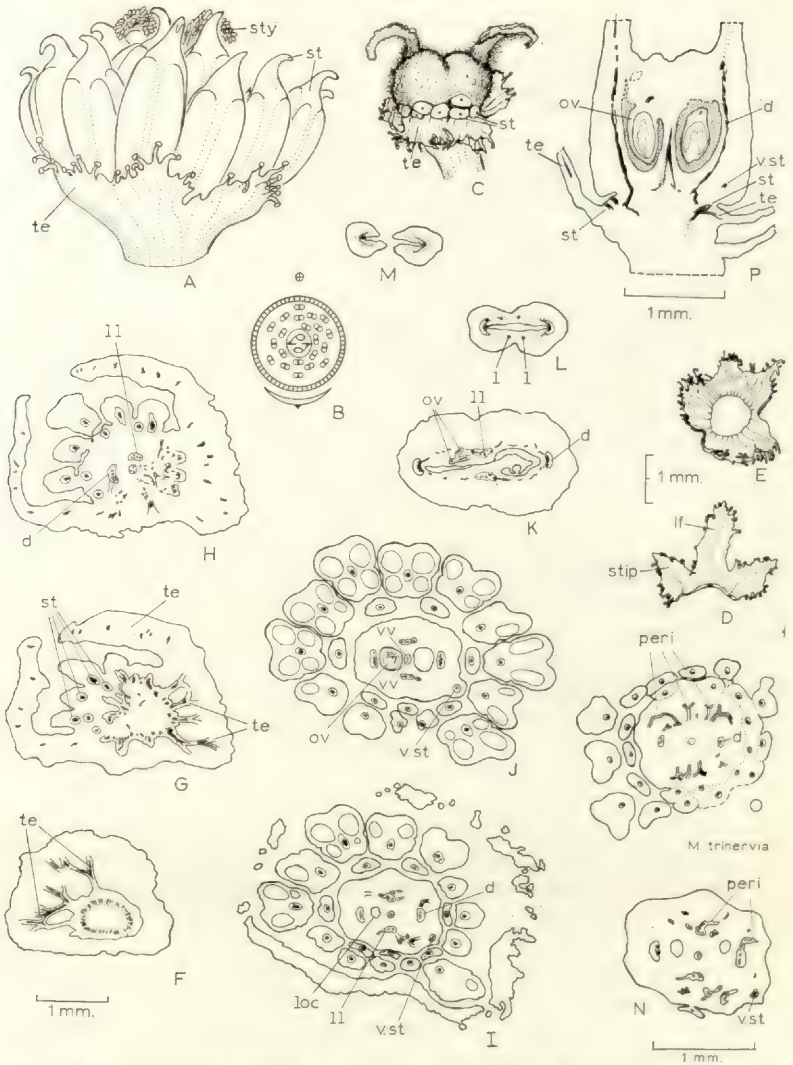

FIGURE 13. **Matudaea hirsuta:** A, flower at anthesis; B, floral diagram; C, post-anthesis flower — note stamen scars crowded beneath the enlarging ovary; D, stipulate primary bract; E, deciduous syntepalous perigon; F-M, transverse sections through a flower at anthesis (slightly oblique); F, pedicellar stele and departing perianth bundles; G, through receptacle, sepal traces departing to right, stamen traces to the left; H, receptacle, part of gynoecial vasculature formed; I, base of one locule — note vestigial stamen trace and some peripheral bundles in the ovary wall; J, about mid-height in the ovary; K, ovule insertion; L, through fused carpels above the ovules; M, through style bases; N, section through ovary just above the level of I, enlarged slightly to show vestigial vasculature; O, section through base of ovary of *M. trinervia* — note vestigial vasculature; P, near-median longitudinal section through an ovary.

hirsuta which I collected in Mexico in 1964. Flowers of *M. trinervia* from herbarium specimens were also examined anatomically, and appear to agree with those of *M. hirsuta*.

MORPHOLOGY: The inflorescences of *Matudaea* are small, congested, and either spicate or paniculate. They are borne in the axils of the two-ranked leaves. Both the leaves and their associated inflorescences become abruptly reduced toward the tip of the shoot axis. The distal leaves may take the form of a much reduced lamina, no larger than its flanking stipules, or of a bract either free from, or variously fused with the two bracteate stipules. At the distal nodes the inflorescences become reduced to a single, short pedicellate, or sessile flower, and the tip of the shoot axis may become similar in appearance to the lateral inflorescences along its length. Larger inflorescences in my collections attain a length of about 2 cm., and bear one or two short secondary axes at the proximal nodes. The secondary axes may bear one or more flowers.

Flowers are situated in the axils of bract-groups which are arranged along the primary and secondary axes in the same one-half phyllotactic sequence as that of the leaves on the shoot axis. The bract-groups represent a reduced leaf and its stipules, an interpretation which is supported both by the obvious reduction of the leaf along the shoot and inflorescence axes, and by nodal anatomy.

There has been much reduction in the inflorescence. Failure of the primary axis to elongate sufficiently at its base results in congestion of proximal secondary axes in the leaf axil, so that two or more axes may appear to have distinct origins in the axil. Failure of internode elongation at the distal end of an axis results in congestion and eventual abortion of subterminal flowers or axes. The compound nature of some few-flowered spikes is frequently indicated by the presence of reduced bracts of the second or third order subtending the flowers of the spike. Congestion in the inflorescences leads to ontogenetic fusions among the various bracteate organs of the axes, particularly between secondary bracts and the syntepalous perigon of the flower.

The flowers are regular, incomplete, and bisexual. The perianth consists of an irregular, syntepalous, circumscissile perigon. The androecium contains 18 to 30 hypogynous stamens, inserted in a congested, shallow ring around the base of the ovary (FIGURE 13C, P). The oblong anthers are subsessile in bud, but strongly exserted at maturity. Each contains four pollen sacs, and dehisces laterally by means of four longitudinal valves. The anther connective is produced as a short apiculus. The two-carpelled superior ovary contains one or occasionally two ovules in each locule. Each carpel terminates in a free, elongate, recurved style, with expanded papillate stigmatic margins.

In bud the perigon forms a cap which tightly encloses the stamens and ovary. At anthesis the cap splits irregularly and longitudinally from an apical pore, expanding to form an irregularly lobed cupulate or reflexed perianth tube (FIGURE 13A, C, E). The margins of the lobes are incised

with many often capitate fimbriae. The tube is shed by means of a circumscissile abscission layer which forms at its base around the rim of the slightly expanded receptacle. There is no morphological indication of the number of tepals incorporated into the tube. In some flowers the stamens appear to be inserted in a more or less spiral fashion, but in others, particularly those with fewer stamens, there is a faint tendency toward an irregularly whorled arrangement approaching three alternating cycles (cf. floral diagram, FIGURE 13B). There is no external evidence of staminodia between the stamens and the ovary.

ANATOMY: The cylindrical pedicellar stele subtending each flower expands rapidly as it enters the receptacle, with some dichotomizing of its bundles. There is little or no regularity or pattern in the vascular supply to the various floral organs. A particular bundle in the receptacle may supply a single organ, or through divisions and anastomoses contribute to more than one

A number of traces (9 to 12) diverge from the pedicellar stele to supply the base of the perianth (te in FIGURE 13F, G). Some of these undergo branching, and the branches of adjacent bundles frequently anastomose, while still within the receptacle. Although usually irregular and complex, the patterns of origin, branching, and anastomosis of the perianth traces in some flowers approach the pattern seen in the nodal anatomy of the foliage leaf (as described in *Distylium*), and suggest the connation of modified stipulate bract groups to form an irregular perigon. In this respect it should be noted that the primary and secondary bracts subtending the flowers have incised margins with capitate fimbriae like those of the perianth lobes (FIGURE 13D, E).

Above the departing perianth traces the supply to the androecium forms. In many cases the stamen trace is formed by the fusion of two bundles in the receptacle, and sometimes of three. Occasionally a single bundle will branch into three, the central trace of which will supply the outer (or lower) of two stamens lying on a given radius, while the two lateral bundles fuse to form the trace to the inner, and morphologically higher, stamen.

As the numerous traces to the androecium diverge, the remaining bundles of the receptacular stele converge centripetally to form the vascular supply to the gynoecium. In transverse section at this level this short internode of the receptacular stele appears as a complex vascular plexus, as seen toward the right side of FIGURE 13H, with part of the gynoecial system evident (dorsal bundle, compound lateral bundle) toward the left side.

In the base of the ovary two dorsal bundles (d), two compound lateral bundles (ll), and a narrow residual receptacular cylinder are apparent. Each of these has a complex and independent origin in the anastomosis of several vascular strands. Also at the base of the ovary one encounters a series of vestigial bundles, suggestive of the peripheral bundles in the ovary of *Distylium*, of which the morphological origins are not known

(peri in FIGURE 13o, of *Matudaea trinervia*, *Standley 25570*). These may be entirely procambial at anthesis, or contain small strands of protoxylem, and appear to branch and anastomose to a certain extent. In flowers of *Matudaea hirsuta* in my collections, similar vestigial bundles were found originating from the bases of the dorsal and compound lateral bundles (FIGURE 13N). These are similar in this respect to certain hypanthial bundles in several genera of petaliferous Hamamelidoideae (Hamamelideae) which are adnate basally to the gynoecial system, but eventually separate to supply organs on the hypanthium.

In the ovary, the residual receptacular stele dichotomizes in the septum just above the base of the locules. The two compound ventral bundles formed ascend to the placentae where each fuses with the adjacent compound lateral bundle. Just prior to this fusion each compound ventral usually provides a single ovule trace to one of the solitary ovules. But ovular traces have also been observed to depart above the point of fusion (FIGURE 13K). Slightly above the level of fusion the compound bundle formed dichotomizes to provide marginal bundles to the style bases.

The inflorescences of *Matudaea* are similar to those of *Distylium racemosum* in their progressive reduction upwards along the shoot, resulting in the merger of inflorescence and shoot distally, and in the abortion of subterminal flowers beneath the terminal flower, due to congestion caused by the failure of the distal internode to elongate. It often appears that in the last stages of its reduction, the subterminal flower develops as a small knot of capitate fimbriae at the base of the terminal flower. But the flowers of *Matudaea* are apparently bisexual, with a definite perianth, rather than unisexual or obviously pseudanthial and atepalous, as in *Distylium*, and there is no direct morphological evidence that the stamens of *Matudaea* are attributable to subterminal naked staminate flowers aggregated about the base of a terminal naked pistillate flower, as in *Distylium*. *Matudaea* thus stands apart from the other apetalous Hamamelidoideae by virtue of its calyptrate perianth and numerous hypogynous stamens, the latter being approached only by the fewer and subperigynous stamens of *Molinadendron*. Its pollen is also distinct, and has apparently not been described in the literature.

Anatomically there is no parallel among the other apetalous genera to the complex vasculature of the perianth. The vasculature of the ovary, like that of *Molinadendron*, is relatively advanced in the fusion of compound ventral and lateral bundles in the placentae, rather than of individual bundles, and in the origin of the ovule trace from the compound ventral, either above or below the level of fusion. The nature of the vestigial vasculature in the base of the ovary is problematical. The presence of a perianth and numerous hypogynous stamens would suggest that these bundles may represent traces to a number of abortive stamens. A specific example of an apparently vestigial stamen, adnate to the base of the ovary and receiving such a trace, is illustrated (v st, in FIGURE 13I, J, N). If this interpretation should prove to be correct, the flower

of *Matudaea* with undifferentiated perianth, numerous hypogynous stamens, and superior ovary, could represent a relatively primitive type, morphologically, among the apetalous Hamamelidoideae. However, the vestigial vasculature is similar to that of *Distylium*, and considered in conjunction with the irregular vascular supply to the perianth, and the similarities of inflorescence morphology, suggests the need for further study and for more information from other areas of investigation before the idea of a pseudanthial origin of the flowers can be discarded entirely.

DISCUSSION

The morphological and anatomical observations recorded above reveal a striking diversity of floral forms and structures which share no common basic pattern. Several parallel lines of specialization appear to be represented, some of which transgress currently recognized generic and tribal limits.

A perianth is absent in *Distylium*, and in those species of *Sycopsis* related to *S. dunnii*. The morphology and vascular supply of the inflorescence and "floral" bracts in these two groups clearly indicate that they represent reduced stipulate leaves. In *Sycopsis sinensis*, *S. griffithiana*, and *Parrotia persica* an irregular perigon of 4 to 10 tepals is inserted on the rim of a shallow to deep hypanthium.[3] The tepals of *Parrotia* are typically more numerous (6 to 10), and more variable in width and length, than those of *Sycopsis sinensis* (4 to 7; cf. Endress & Anliker 1968, *figs. 3, 4*), usually appearing as distinct bracts rather than as irregular lobes of a syntepalous perigon tube as in *Sycopsis sinensis* and *S. griffithiana*. The perianth in the latter species appears to represent only a modified form of that seen in *Parrotia*, with increased fusion among the tepals to form the perigon tube beyond the rim of its longer hypanthium. The 5 to 8 tepals of *Fothergilla*, although smaller in size, are similar to those of *Parrotia* and *Sycopsis sinensis* in their variable width and irregular vascular supply, and may represent a modification from a perigon similar to that of *Parrotia*. Such reduction may be observed also in the minute, irregular tepals of *Parrotiopsis*, which are so poorly developed that little can be said about their vascular supply.

In the androecia of all seven genera the stamens are variable in number and insertion relative to the members of the perianth, and are strongly exserted. The 18 to 30 hypogynous stamens of *Matudaea* would appear to mark this genus as rather unspecialized among the apetalous taxa. It is not clear whether the large numbers of perigynous stamens on the hypanthia of *Fothergilla* (12 to 32) and *Parrotiopsis* (21 to 25) are derived from a many-stamened, hypogynous ancestor similar to Matudaea, or whether they have developed secondarily from an ancestral type, per-

[3] The reader is reminded that the term hypanthium is used here only in a descriptive sense, and he is referred to the section on General Considerations, above, for a brief discussion of the morphological nature of the hypanthium in the Hamamelidoideae.

haps similar to *Parrotia* (8 to 15). The seven to ten stamens inserted around the narrower mouth of the hypanthium in *Sycopsis sinensis* probably represent a slight reduction from a larger ancestral number on a more extensive hypanthium rim, such as that seen in the closely related *Parrotia persica*. Three to seven perigynous stamens have been counted in *Sycopsis dunnii*, while two to six stamens occur in the subperigynous flowers of *Molinadendron*, and in the staminate flowers of *Distylium*.

Anthers vary in size and shape among the genera from small and slightly oblong (*Fothergilla*, *Parrotiopsis*) to large and linear-oblong (*Parrotia*, *Sycopsis sinensis*). The anther connective is barely, if at all, produced as an apiculus in *Fothergilla* and *Parrotiopsis*, and slightly to moderately produced in the other genera, becoming longest in *Matudaea*, *Parrotia*, and in the male flowers of *Sycopsis sinensis*. Dehiscence is by means of four more or less distinct valves in *Fothergilla*, *Parrotiopsis*, *Matudaea*, and *Molinadendron*, by slits which tend toward a subvalvate condition in *Distylium* and several species of *Sycopsis*, and by simple slits in *Sycopsis sinensis* and *Parrotia*. Although the flowers and stamens of these apetalous genera are presumably modified for wind pollination, the conspicuous white involucral bracts surrounding the inflorescence of *Parrotiopsis*, and the dense clusters of long, white, clavate stamen filaments in *Fothergilla*, suggest adaptations toward visual attraction of insect pollinators. Unfortunately, observations regarding such characteristics as floral fragrance and pollinators are lacking in the literature.

A hypanthium is absent in *Matudaea* and *Distylium*, and only weakly developed in *Molinadendron*, where it is more obvious around the base of the mature fruit. The shallow hypanthium of *Parrotia* is free of any fusion to the ovary wall, but the hypanthia of *Fothergilla* and *Parrotiopsis* are partially adnate to the base of the ovary. The tubular hypanthium of *Sycopsis sinensis* probably represents an elaboration of a shallower ancestral type, such as that of *Parrotia*, but the morphological nature of the more or less urceolate hypanthium in *Sycopsis dunnii* and its related species is not entirely clear. It may represent the fused tissues of reduced stipulate leaves, and associated axillary axial and floral tissues into a tube around an ovary, and may not be homologous at all with the hypanthium of *Sycopsis sinensis*.

The general characteristics of the gynoecium in the subfamily Hamamelidoideae have been described above (see General Considerations). Among the apetalous genera the position of the ovary ranges from superior to partially inferior. The pistil of *Distylium* is apparently superior morphologically, but the presence of a vestigial peripheral bundle system in its base, in conjunction with the absence of a perianth and androecium, suggests the possibility that it may be only secondarily superior. A vestigial system of peripheral bundles is also present in the base of the superior ovary of *Matudaea*, but in the presence of a perianth and androecium this vasculature may represent vestigial traces to abortive stamens. The superior ovaries of *Sycopsis sinensis* and *Parrotia*, although lacking well developed vestigial bundle systems, are associated with other morph-

ological and anatomical peculiarities which suggest a relationship to *Distylium*, and the possibility that their ovaries may also be secondarily superior. The ovary of *Fothergilla* varies from more or less hypogynous to one third inferior (cf. Weaver 1969), while in the closely related *Parrotiopsis* the lower fourth or third of the ovary is adnate with the proximal portion of the hypanthium. The pistil of *Molinadendron* is sessile and slightly inferior in an expanded receptacle.

Considering only the evidence of floral morphology a general trend of floral development among the apetalous Hamamelidoideae could be hypothesized to have progressed from a relatively primitive, bisexual flower, containing a perianth consisting of a variable number of undifferentiated tepals, numerous hypogynous stamens, and a superior bi- or tricarpellary ovary, essentially as in *Matudaea* (which differs in having the tepals fused in a tubular perigon). From this basic plan could be derived forms in which the tepals and stamens have become fused basally into a shallow, hypogynous hypanthium (*Parrotia*, *Fothergilla*), possibly accompanied by reduction in stamen number (*Molinadendron*, *Parrotia*, *Sycopsis sinensis*), and partial adnation of the hypanthium to the ovary (*Fothergilla*, *Parrotiopsis*). Elaboration of the hypogynous hypanthium into an urceolate tube, possibly accompanied by reduction and loss of the tepal lobes morphologically (*Sycopsis dunnii* and related species), and suppression of the development of the gynoecium in lateral flowers of the inflorescence axes (*Sycopsis dunnii*), or in some whole inflorescences (*Sycopsis sinensis*), would lead to more advanced andromonoecious floral types (*Sycopsis*). Finally, suppression of the hypanthium and its associated perianth lobes (if present) would lead to terminal naked pistillate flowers and lateral naked staminate flowers (*Distylium*). The vestigial vasculature in the base of the pistil of *Distylium* would then be attributable to the lost hypanthium, rather than to lost stamens as hypothesized for *Matudaea*. This sequence appears reasonable with regard to the progressive steps of modification necessary to derive the various floral forms involved. It differs from that proposed by Tong (1930) and Harms (1930) in that they derived the polygamous, apetalous genera of the tribes Fothergilleae and Distylieae from a petaliferous ancestral type through the transformation of petals into stamens, rather than from an apetalous ancestral type such as *Matudaea*, which was unknown at that time.

In such a series the flowers would represent euanthia, and the morphological nature of the perigon, lacking only in *Distylium* and those species of *Sycopsis* related to *S. dunnii*, and of the hypanthium, would be homologous. If correct, the apetalous genera of Hamamelidoideae may represent the remnants of a line of floral specialization quite apart from that which gave rise to the petaliferous genera, for *Matudaea* has no close morphological counterpart among the petal bearing members of the subfamily. Among the latter group, on the basis of accumulated evidence of wood anatomy, pollen morphology, floral morphology, and floral vascular anatomy (personal observations, in manuscript), the most

primitive genera appear to be *Maingaya* Oliv. and *Dicoryphe* Thou. Their pentamerous (or tetramerous in some species of *Dicoryphe*) flowers contain alternating cycles of sepals, petals, 5(–4) stamens, 5(–4) large staminodia which approach the stamens in shape, and an inner cycle of 10(–8) scales or lobes, all inserted perigynously on the rim of a tubular hypanthium above a half-inferior or essentially inferior ovary.

However, in view of the unusual features of floral morphology and vascular anatomy in *Distylium*, *Sycopsis*, and *Parrotia*, it may be worth considering another, more speculative, interpretation of the course of floral development among at least some of the apetalous genera, leading from a hypothetical unisexual, monoecious, ancestral type, to bisexual pseudanthia through the condensation of inflorescences and the aggregation of staminate and pistillate flowers within a cycle of bracts. Among extant genera the species of *Distylium* could represent an early stage in the development of such pseudanthia. Its naked unisexual flowers have probably been derived from those of a bisexual ancestor through the suppression of the perianth and gynoecium in the case of the lateral staminate flowers, or of the perianth and androecium in the terminal pistillate flowers on each inflorescence axis. Such reduction must be assumed regardless of the phylogenetic sequence in which the genus is placed. The vestigial vasculature in the base of the terminal functional ovaries is evidence of the former presence of such organs. In this genus the condensation of inflorescence axes and the aggregation of bracts and staminate flowers around a terminal pistillate flower have already produced a condition in which the external identity, and even the anatomical identity, of the individual flower is lost, and the inflorescence merges into a false flower.

From a common ancestor with unisexual flowers more or less similar to those of the present day distyliums, the apparently bisexual flowers of *Sycopsis dunnii* and its related species may have developed through a more pronounced reduction of inflorescences axes, resulting in the aggregation and fusion of lateral trimerous primary bract groups with their associated axillary axial tissues and staminate flowers into a tubular false hypanthium around a naked terminal pistil.

From a similar hypothetical ancestor, the capitate inflorescences and bisexual flowers of *Parrotia* could have evolved through the condensation of entire lateral inflorescence axes, resulting in the aggregation and fusion of a variable number of primary bract groups and highly modified lateral staminate flowers in a shallow hypanthium around the persistent naked terminal pistil.

From a condition such as that seen in *Parrotia* it is only a short step, in one direction, to *Sycopsis sinensis* through a lengthening of the hypanthium, with concomitant reduction in the number and size of "tepals," and in the number of stamens developed on its narrowed rim. The morphological origins of the hypanthium of *S. sinensis* would then appear to differ somewhat from those of the similar structure in *S. dunnii*, and the two species would represent an interesting case of phylogenetic

convergence, resulting in urceolate hypanthia that are ruptured by the developing fruit. In another direction could be derived *Fothergilla* and *Parrotiopsis*. In these genera the increased number of stamens may represent either the retention of an ancestral condition or a secondary development.

In the context of a pseudanthial interpretation, the flowers of *Matudaea* might represent a less advanced New World counterpart of *Parrotia*, its aggregated connate bracts not yet having become fused in a hypanthium with the stamens. The vestigial vasculature in the base of the ovary, like that in *Distylium*, might then be attributable to a phylogenetically lost floral envelope which once surrounded the ovary. In *Molinadendron*, on the other hand, the irregular relationships and variable numbers of the stamens and one-trace tepals are suggestive of an aggregation of bracts and stamens similar to those seen in some highly reduced inflorescences of *Distylium buxifolium*.

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ARNOLD ARBORETUM
HARVARD UNIVERSITY

A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

S. M. A. Kazmi

8. **Pseudomertensia** Riedl in Rechinger, Fl. Iranica **48**: 58. 1967.

Oreocharis (Decne.) Lindl. Veg. Kingd. 656. 1848, *non* Benth. 1876, *pro parte.*
Lithospermum L. subgen. *Oreocharis* Decne. in Jacquem. Voy. Inde Bot. 122. 1844, *pro parte.*
Eritrichium Schrad. sect. *Oreocharis* (Decne.) DC. Prodr. **10**: 123. 1846, *pro parte.*
Mertensia auct. fl. asiatica *pro parte* — non Roth, Catalecta **1**: 34. 1797.

Type species: *Lithospermum elongatum* Decne.

Perennial, strigose or softly hairy herbs. Leaves usually alternate. Racemes terminal, scorpioid, usually simple, dense or lax, ebracteate. Flowers blue to purplish-blue, pedicellate. Sepals narrow, sometimes enlarged in fruit. Corolla campanulate, cylindrical-campanulate, or hypocrateriform; tube as long as, or much longer than the calyx; throat with or without appendages; lobes 5, imbricate in bud, short, spreading or erect. Stamens 5, included or exserted from the corolla tube; filaments very short to very long; anthers oblong, obtuse, or rarely acute. Ovary 4-lobed, style filiform, stigma capitate, small. Nutlets 4, erect, ovoid-oblong, dorsally slightly convex, ventrally carinate, slightly angular, margins often acute; areola distinct, sub-basal, oblique, affixed to the short pyramidal gynobase.

Species 11 to 12, distributed in Western Himalayas from Afghanistan to Nepal.

Key to the Species

a. Anthers exserted from the corolla tube, filaments 2–5 mm. long.
  b. Corolla more or less equalling the calyx; corolla lobes up to 1.5 mm. long, faucal appendages absent. ..... 1. *P. parviflora.*
  b. Corolla much exceeding the calyx; corolla lobes 2.5–3 mm. long; faucal appendages present. ..... 2. *P. trollii.*
a. Anthers included or little exserted from the corolla tube; filaments less than 2 mm. long.
  c. Faucal appendages absent.
    d. Corolla not constricted at the throat; internally with minute pubescence instead of faucal appendages; filaments 2 mm. long. ..... 3. *P. efornicata.*
    d. Corolla constricted at the throat, internally glabrous; filaments hardly up to 0.5 mm. long. ..... 4. *P. echioides.*
  c. Faucal appendages present, poorly to well developed.

* Continued from volume 51, p. 184.

e. Corolla campanulate. ..... 5. *P. elongata.*
e. Corolla not campanulate; distinctly cylindrical or infundibuliform.
f. Faucal appendages longer than broad.
g. Faucal appendages 2–3 mm. long, 1–1.5 mm. broad at the base, triangular, ciliate at the margins. ..... 6. *P. drummondii.*
g. Faucal appendages 0.8–1.2 mm. long, 0.5 mm. broad at the base, lingulate, not ciliate at the margins. .. 7. *P. chitralensis.*
f. Faucal appendages broader than long.
h. Filaments usually longer, rarely equalling the anthers in length. ..... 8. *P. anjumiae.*
h. Filaments always shorter than the length of anthers.
i. Leaves, including petioles, 40–160 mm. long, 10–45 mm. broad; corolla tube twice as long as the calyx, anthers up to 1 mm. long. ..... 9. *P. nemorosa.*
i. Leaves, including petioles, 15–80 mm. long, 2–10 mm. broad; corolla tube three to five times as long as the calyx; anthers 1–1.7 mm. long. ..... 10. *P. moltkioides.*

1. **P. parviflora** (Decne.) Riedl in Rechinger, Fl. Iranica **48**: 60. 1967.

Craniospermum parviflorum Decne. in Jacquem. Voy. Inde Bot. **1**: 126. *t. 130.* 1844.

Moltkia parviflora (Decne.) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 171. 1883.

Mertensia exserta I. M. Johnston, Jour. Arnold Arb. **37**: 305. 1956; R. R. Stewart, Biologia **13**: 93. 1967.

TYPE: In summis pascuis à Ilahabad ad Hyderabad trans jugum Pirpenjal, 2681 m., *Jacquemont s.n.* (P).

ICON.: Jacquemont, l. c. *t. 130.* 1844.

Perennial with stout woody underground rhizomes; emerging shoots many, suberect or sometimes trailing, 6–15(–25) cm. long, clothed with short appressed trichomes. Basal leaves short petiolate, linear-oblong, entire, obtuse or subacute, 40–50 mm. long, 4–6 mm. broad, covered on both surfaces with short, appressed trichomes; cauline leaves mostly sessile, shorter and narrower, acutish. Inflorescence usually forked, sometimes simple, short and scorpioid when young, later elongated, curved, 2–6 cm. long. Calyx divided to the base, lobes narrow oblong, 2.5–3 mm. long, densely hairy on the lower parts and margins, obtusish, in fruits slightly enlarged; pedicels 1–4 mm. long. Corolla 2.5–3 mm. long, more or less equalling the calyx, cylindrical, glabrous, tube 2–2.5 mm. long, lobes 0.5–1(–1.5) mm. long, 0.5–0.8 mm. broad at base, erect. Stamens much exserted from the corolla tube; anthers obtusish, elliptic, 0.5–0.6 mm. long, versatile; filaments up to 3 mm. long, inserted about 2.5 mm. above the corolla base. Style 6 mm. long, stigma minute, subcapitate. Nutlets ovoid-oblong, acute, smooth, shining, ca. 2 mm. long.

DISTRIBUTION: West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Ziarat, Lowari Pass, 2600 m., *Stainton 2337* (BM). HAZARA DIST.: Pipe line, Changlagali, 2500–3000 m., *Dickason 83*

(MICH); between Dungagali and Changlagali, 2500–3000 m., *Kazmi 746a* (PES); Nathiagali, 2700 m., *Kazmi 84b* (PES). KURRAM AGENCY: Kurram Valley, *Afandi 404* (PES); Ziran, *Kazmi 207a* (PES); Shalozan, *Kazmi s.n.* (PES), *Afandi s.n.* (PES); Kaiwas & Shendtoi, 2700–3000 m., *Aitchison 397* (GH). RAWALPINDI DIST.: Murree Hills, 2300 m., *R. R. Stewart 12559* (GH), *Asghar Ali, s.n.* (MICH); Patriata Forest, *Kazmi 4c* (PES); Murree, Kashmir Point, *Kazmi 2480* (PES); Upper Topa, *Kazmi 2487* (PES).

Kashmir: Poonch, Trarkhel, 2000 m., *R. R. Stewart 12084* (GH); Gulmarg, *Aitchison 74* (K), *Keshawanand 1162* (GH), *Trotter 110* (BM); Basin of Chenab, *Thomson* (4. 5. 1848) *s.n.* (K); near Avantipura, *Thomson* (4. 5. 1848) *s.n.* (K); Lidder Valley, Kinimola Nulla, *Inayat 25705* (K). Miscellaneous: 5000–7000 ped., Herb. Ind. Orient. Hook. f. & Thoms., *Thomson s.n.* (GH).

2. **P. trollii** (Melch.) Stewart & Kazmi, comb. nov.

Mertensia coventryana S. Clay, The Present Rock Garden **20:** 379. *t. 27a.* 1937, *nomen nudum.*

Moltkia trollii Melch. Notizbl. Bot. Gart. Berlin **15**(1): 115. 1940.

Mertensia trollii (Melch.) I. M. Johnston, Jour. Arnold Arb. **37:** 303. 1956; Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 227. 1963.

TYPE: Kashmir: Tragbal Pass, in der Nadelwaldregionen mit *Pinus, Picea* und *Abies,* 3000 m., Blüten hellblau, *C. Troll 7028* (B).

ICON.: S. Clay, l. c. *t. 27a.* 1937, under *Mertensia coventryana.*

Perennial with underground branched rhizomes to 20 cm. long; emerging shoots usually curved, sometimes erect, to 10 cm. tall, clothed with short, thick, white, appressed trichomes. Basal leaves including petioles 4–6 cm. long, 4–18 mm. broad, lamina elliptic or elliptic-oblong, entire, apices obtuse, glandular, nerves prominent below, at the base gradually attenuated into long petioles, more or less ciliate at margins, broad at the base; both surfaces covered with short, white, appressed trichomes, cauline leaves oblong to oblong-lanceolate, shorter, narrower, sessile to subsessile. Inflorescence terminal, usually solitary, contracted, scorpioid, 1–3 cm. long. Calyx shorter or equal to the corolla tube, divided to the base, lobes linear-oblong, acute, densely hairy on the margins, few scattered trichomes externally, marginal trichomes 0.5–0.8 mm. long and antrorsely spreading; pedicels 1–3 mm. long. Corolla sky-blue to dark purplish-blue, 7–8 mm. long, glabrous, tube cylindrical ca. 5 mm. long, lobes oblong, 2.5–3 mm. long, ca. 1.8 mm. broad at the base, subpatent; faucal appendages 0.5 mm. long and broad. Stamens exserted from the corolla tube to exceeding the corolla lobes; anthers versatile, elliptic, obtuse, 1–1.5 mm. long; filaments 2.5–5 mm. long, slightly narrowed at the apices, inserted at the level of the faucal appendages, about 4 mm. above the corolla base; style filiform, equalling or shorter or little exceeding the stamens; stigma minute, subcapitate.

This species is closely related to *Pseudomertensia parviflora* in having stamens conspicuously exserted from the corolla tube, but differs from it in having a much longer corolla with well developed lobes and five in-

vaginated hemispheric appendages in the throat. The corolla lobes in *P. trollii* are oblong or elliptic, 2.5–3 mm. long and clearly exceeding the calyx lobes, while those of *P. parviflora* are more or less triangular and usually 1–1.5 mm. long.

The length of calyx, corolla, filaments, and anthers is very variable in *Pseudomertensia trollii* and the three following varieties may easily be distinguished.

KEY TO THE VARIETIES

a. Calyx about 2/3 the length of corolla tube; corolla 9–11(–12) mm. long. . . . . 2c. var. *edelbergii*.
a. Calyx usually equal to the corolla tube; corolla up to 8 mm. long.
  b. Anthers 1 mm. long; filaments 4–5 mm. long; faucal appendages well developed. . . . . 2a. var. *trollii*.
  b. Anthers 1–1.5 mm. long; filaments ca. 2 mm. long; faucal appendages poorly developed. . . . . 2b. var. *harrissii*.

2a. Var. **trollii**.

Basal leaves narrower and with short petioles compared to var. *edelbergii*; calyx more or less equal to the corolla tube; corolla up to 8 mm. long, lobes acutish; anthers 1 mm. long; filaments 4–5 mm. long.

DISTRIBUTION OF VAR.: West Pakistan, Kashmir.

West Pakistan: GILGIT AGENCY: On Indus river near Rondu, E–W. of Skardu, about 40 miles, *Thomson* (18.3.1848) *s.n.* (K); Gurais, *Mrs. Earl* in *R. R. Stewart 1258* (GH). HAZARA DIST.: Kaghan Valley, Bhimbal, 2300 m., *Duthie 19486/a* (K); Batakundi, 2700 m., *Champion* (13.5.1927) *s.n.* (GH); *Kazmi s.n.* (PES).

Kashmir: Tragbal Pass, 3000 m., *Troll 7028* (B-type); Kajnag range, *Duthie 11073* (E); Banihal Pass, 3000 m., *Coventry 1448* (BM); Pahlgam, 3000 m., *Miss Ward 116* (BM).

2b. Var. **harrissii** Kazmi, var. nov.

TYPE: West Pakistan: Dir, *Harriss 16397* (GH-holotype).

Folia basalia ad var. *trollium* similia; tubum calycis corollae plus minusve aequans; corolla usque ad 8 mm. longa, lobi aliquot obtusi; antherae 1–1.5 mm. longae; filamenta 2.5 mm. longa.

DISTRIBUTION OF VAR.: West Pakistan.

West Pakistan: DIR STATE: Dir, *Harriss 16397* (GH-*type*). HAZARA DIST.: Naran, near the Ganji Pahari top, 3000 m., *Kazmi 2218b* (PES); Saiful Maluk Sar, *D. McVean* (June 1960) *s.n.* (E); between Dadar and Kaghan (probably at Shahid Pani ?), *Inayat 22006* (K).

2c. Var. **edelbergii** (Rech. f. & Riedl) Kazmi, comb. nov.

Mertensia edelbergii Rech. f. & Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 230. *t. 176, 177.* 1963.

Pseudomertensia edelbergii (Rech. f. & Riedl) Riedl in Rechinger, Fl. Iranica **48**: 60. 1967.

TYPE: Afghanistan: Nuristan: Pashki, 2300 m., *Edelberg 630* (W-holotype, C-isotype).

ICON.: Riedl l. c. *t. 176, 177.* 1963.

Basal leaves broader with longer petioles as compared to the other two varieties; calyx about *2/3* the length of the corolla tube; corolla 9–11(–12) mm. long; anthers ca. 1 mm. long; filament 2.5 mm. long.

DISTRIBUTION OF VAR.: West Pakistan, Afghanistan.

West Pakistan: SWAT STATE: Kalam, 3000 m., *Kazmi 2468* (PES); Indus Kohistan, beyond Ushu, 3200 m., *Kazmi s.n.* (PES); Kalam mountain, S–E. of village, upper section of hill above 'alp' rocks, near ridge, flowers deep blue fading to deep pink, 3000–3200 m., *Lamond 1841* (E); *Lamond* in *Rechinger 30854* (W).

Rechinger and Riedl (*l. c.* 1963) in their original description of *Pseudomertensia edelbergii* gave the length of the corolla as 9–11(–12) mm.; later Riedl (*l. c.* 1967) cited the length of the corolla as 7–8 mm. which is the length of the corollas in varieties *trollii* and *harrissii*. In all the specimens of var. *edelbergii* cited above, the length of the corolla is definitely more than 8 mm. Also, the original description of *P. edelbergii* does not indicate the length of the filaments, which was measured by me to be more or less 2.5 mm., much shorter than the length of the filaments of *P. trollii*, but almost the same as in var. *harrissii*, from which var. *edelbergii* differs in having a shorter calyx in comparison with the length of the corolla tube, as well as shorter anthers and larger leaves. Both var. *edelbergii* and var. *harrissii* differ from the typical variety in the length of the filaments which varies between 4 and 5 mm. Because the length of the filaments in the *P. trollii* complex is not very constant, and since var. *harrissii* represents an intermediate form between *P. edelbergii* and *P. trollii*, I consider all three taxa as only varieties of *P. trollii*.

3. **P. efornicata** (Rech. f. & Riedl) Riedl in Rechinger, Fl. Iranica **48**: 60. 1967.

Mertensia efornicata Rech. f. & Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 231. 1963.

TYPE: Chitral, Drosh, 11500 ft., *Bowes Lyon 186* (BM).

ICON.: Riedl, l. c. *232. fig. 178.* 1963, under *Mertensia efornicata.*

Perennial; rhizomes stout, long, more or less 1 cm. thick, branched, branches short, underground; emerging shoots many, 18–25 cm. long, erect, simple, or in the upper parts, bifurcate, covered loosely with patent to subappressed trichomes. Basal leaves lanceolate to oblong lanceolate, apices apiculate, attenuated at the base into petioles, including the petioles 5–12 cm. long, 7–18 mm. broad, on the lower surface thickly,

on the upper surface loosely covered with short trichomes; upper leaves few, attenuated towards the base, sessile, 2–4 cm. long, 3–8 mm. broad. Inflorescence solitary, short when young, later elongated up to 10 cm., bearing many distant pedicellate flowers; pedicels 3–5 mm. long. Calyx divided to the base, lobes linear, acute, ± 5 mm. long, 0.5–0.7 mm. broad, loosely covered with subappressed short trichomes. Corolla 10–11 mm. long, cylindrical-campanulate, glabrous externally, minutely hairy internally in the throat in place of faucal appendages, throat not constricted, lobes and tube not distinct, lobes ovate to roundish, 2–2.5 mm. broad. Anthers ± 1.5 mm. long, sagittate, acute, slightly exceeding the sinuses between the corolla lobes; filaments filiform, 2 mm. long, attached 5–6 mm. above the corolla base. Style filiform, equalling or slightly exceeding the corolla; stigma capitate.

DISTRIBUTION: West Pakistan.

West Pakistan: CHITRAL STATE: Drosh, Painogh, 3500 m. (13. 7. 1958), *Bowes Lyon 186* (BM).

The absence of faucal appendages brings *P. efornicata* very close to *P. echioides* but the presence of pubescence in place of them distinguishes this species from the latter. In *P. echioides* the anthers are subsessile or the filaments never exceed the length of 0.5 mm., whereas in *P. efornicata* filaments are about 2 mm. and always longer than the anthers.

4. **P. echioides** (Benth.) Riedl in Rechinger, Fl. Iranica **48**: 62. 1967.

Lithospermum echioides Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1839; DC. Prodr. **10**: 63. 1846.

Lithospermum secundiflorum Decne. in Jacquem. Voy. Inde Bot. 120. 1844.

Eritrichium secundiflorum (Decne.) A. DC. Prodr. **10**: 124. 1846.

Mertensia echioides (Benth.) Benth. & Hook. f. Gen. Pl. **2**: 857. 1873; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 170. 1883; Riedl in Køie & Rechinger, Biol. Skr. **13**(4): 229. 1963.

Mertensia secundiflora (Decne.) Brand, Pflanzenr. IV. **252**(Heft 97): 200. 1931.

Mertensia strigosa Melch. Notizbl. Bot. Gart. Berlin **15**: 113. 1940, *syn. nov.*

TYPE: Soongnum in Kunawar-Kherang Pass, *R. Inglis s.n.* (K).

ICON.: Riedl, l. c. *fig. 175.* 1963, under *Mertensia echioides.*

Perennial with long underground rhizome. Emerging shoots usually erect, sometimes decumbent or curved, 5–20 cm. long, clothed with short usually spreading, rarely appressed, thin trichomes. Basal leaves including long petioles (25–)40–90(–150) mm. long, (5–)10–15(–25) mm. broad; lamina ovate, elliptic-lanceolate or lanceolate, usually acute, sometimes obtuse, margins entire, covered on both surfaces thinly or densely, and at the margins with longer, up to 1 mm. long trichomes, arising from tuberculate bases and sometimes curved at their tips; upper cauline leaves few, shorter and narrower, sessile. Inflorescence short and scor-

pioid when young, later elongated up to 13 cm., lax, bearing 10–20 subsessile pedicellate flowers to 10 mm. apart; pedicels up to 3 mm. long. Calyx divided to the base, lobes linear, ± obtuse, erect, 4–5 mm. long, 0.5 mm. broad at base. Corolla blue to deep purple-blue, subcylindrical to funnel-shaped, glabrous, bearing few trichomes at the sinuses between the lobes; corolla tube 4.5–6 mm. long, slightly dilated above; lobes usually 3–4.5 mm., sometimes even longer, 1.5 mm. broad; faucal appendages absent. Anthers oblong, acute or rarely emarginate at the apices, usually emarginate or roundish at base, 1.5–1.9 mm. long exserted from the corolla tube, sometimes anther tips reaching half the length of the corolla lobes; filaments not more than 0.5 mm. long, thick, attached 4.5–5.5 mm. above the corolla base. Style 10–12(–15) mm. long, filiform; stigma capitate. Nutlets ovoid–trigonal, acute, pubescent on ridges, 1.8–2.5 mm. long, 1–1.5 mm. broad.

DISTRIBUTION: West Pakistan, Kashmir, and India.

Most authors have placed *Pseudomertensia echioides* with the species having faucal appendages and have distinguished it from those species because the appendages are less developed and the anthers are exserted from the corolla tube. With these characters it becomes sometimes quite difficult to distinguish *P. echioides* from the allied species, which have faucal appendages at various stages of development and anthers usually exserted from the corolla tube. In the specimens, including the type, which I have examined, I found that *P. echioides* has no faucal appendages, and if very rarely these are present, they are in indistinct traces. Anthers are subsessile and the filaments never exceed 0.5 mm. in length; filaments are thick and dilated at the base. These characters are well correlated with the long (1.5–1.9 mm.) anthers, usually acute at their apices, with usually slightly produced connectives and with the presence of trichomes at the sinuses between the corolla lobes. The presence of trichomes at the sinuses is not found in any other species of our area.

The size and form of the leaves of *Pseudomertensia echioides* are very variable and two varieties may be distinguished easily.

4a. Var. **echioides.**

Shoots few, not profusely leafy, leaves thick, usually oblong-lanceolate, up to 1.5 cm. broad, densely covered with trichomes; inflorescence more compact and less hairy in comparison to var. *lahulensis*.

DISTRIBUTION OF VAR.: West Pakistan, Kashmir.

West Pakistan: GILGIT AGENCY: Astor valley, Kalapani, Kamrinala, *Inayat 25708* (K); Shankargarh above Astor village, *Giles 66* (K); Astor to Degru, *Conway 334* (K); Upper Shingu valley, Deosai region, 3000 m., *R. R. Stewart 22231* (GH); Baltistan, Satpara Nullah, 3000 m., *Webster & Nasir 6356* (GH), 3500 m., *R. R. Stewart 20244* (GH, MICH, US), 3000 m., *Siddiqui, Nasir & Zaffar Ali 4231* (BM, RAW), *Duthie* (12. 7. 1892) *s.n.* (BM); Nathar waterfall,

R. R. Stewart 26343 (RAW); near Skardu, 2300–2500 m., *Schlagintweit 794* (BM); Marpu Nullah, above Dras, 4000 m., *Duthie* (3. 7. 1892) *s.n.* (BM); Burja La, 4000 m., *C. B. Clarke 29930* (BM, K).

Kashmir: Shakkar, Rangdum, 4000 m., *Koelz 5969* (GH, MICH, US); Barnaj Nullah, near Sapphire Mines, Kishtwar, 3500 m., *Ludlow & Sherriff, 9181* (GH); Suru valley, N. of Srinagar, 4000 m., *Osmaston 212* (K); LADAKH: Hanu Yegma via Handamir up to Chorbat La Pass (Pass between the Indus valley and the Shayek valley), *Schlagintweit 6511* (US). Miscellaneous: Hab. Himal. Bor. Occ., 5000–6000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH, US), *Falconer s.n.* (GH).

Mertensia strigosa Melch. agrees in all its details with *Pseudomertensia echioides* var. *echioides* and represents only a more densely pubescent form of the variety.

4b. Var. **lahulensis** (Brand) Kazmi, comb. nov.

Lindelophia lahulensis Brand, Repert. Sp. Nov. **19:** 70. 1923.

TYPE: Lahul: Kyelang, an Felsen des Nyimephed, 4200 bis 4400 m. U.M., im Juli, 1880, *Heyde s.n.* (ZI — Herb. Bernhard Lorenz).

Shoots many, profusely leafy, leaves thin, usually ovate to ovate-lanceolate, more than 1.5 cm. broad, loosely covered with trichomes; inflorescence lax; fruits more hairy than in var. *echioides*.

DISTRIBUTION OF VAR.: INDIA (Lahul): Kyelang, *Koelz 470, 5183, 8408* (GH, MICH, US).

5. **P. elongata** (Decne.) Riedl in Rechinger, Fl. Iranica **48:** 61. 1967.

Lithospermum elongatum Decne. in Jacquem. Voy. Inde Bot. 121. 1844.
Mertensia elongata (Decne.) Benth. & Hook. f. Gen. Pl. **2:** 857. 1873; C. B. Clarke in Hook. f. Fl. Brit. India **4:** 173. 1883.
Eritrichium elongatum (Decne.) A. DC. in DC. Prodr. **10:** 124. 1846.

TYPE: KASHMIR: Supra Pendjegram, 2600 m., Aug. 21, 1831. *Jacquemont s.n.* (GH, P).

ICON.: Jacquemont, l. c. *t. 126.* 1844.

Perennial with underground rhizomes 10–15 cm. long and 0.5 cm. thick. Emerging shoots simple, greenish-white, erect, 10–25(–30) cm. tall, covered densely with antrorse, appressed to subappressed, white, trichomes up to 0.7 mm. long, rarely longer. Basal leaves petiolate; petioles up to 30 mm. long, margins ciliate, base broad, clasping the shoots; lamina oblong to oblong-lanceolate, narrowed at both ends, entire, acute, 15–50 mm. long, 6–8 mm. broad, covered on both surfaces, below comparatively densely, with thin appressed trichomes, usually arising from minute tuberculate bases; middle cauline leaves sessile or subsessile, to 70 mm. long, and 12 mm. broad; upper cauline leaves sessile and shorter than the middle ones. Inflorescence solitary, short and scorpioid when young, later elongated, 2–6(–9) cm. long, bearing 5–15 closely set (to 6 mm.

distant) flowers; pedicels of the lower fruits up to 6 mm. long, gradually decreasing in size upwards, hairy. Calyx 3–5(–5.5) mm. long, divided to the base, lobes linear, acute, erect, up to 0.5 mm. broad, covered sparsely dorsally and densely at the margins with thin, white, subappressed or rarely patent trichomes. Corolla blue, bluish-purple, or deep blue, campanulate, (6–)7–9(–9.5) mm. long, glabrous, tube equal or slightly longer than the calyx, gradually extended from the base; lobes roundish, patent, 2.5–3.5 mm. long and 2–3 mm. broad at the base; faucal appendages poorly to well developed, 3–3.5 mm. above the corolla base, the area above the appendages usually puberulous. Anthers 1.5–2 mm. long, oblong, acute, emarginate at bases, 1.5–2 mm. long; filaments 0.5–1.5 mm. long, thick, attached 2.5–3.5 mm. above the corolla base. Nutlets 4, glabrous, smooth, shining, acute, ovoid-trigonal, pallid, 2.5 mm. long, 1.5–1.6 mm. broad.

DISTRIBUTION: West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Shishi Kuh, 2700 m., *Harriss s.n.* (BM). GILGIT AGENCY: Babusar village, 4200 m., *Siddiqui 2727a* (MICH).

Kashmir: East of Pirpanjal, above Tilpatra forests near Rampur, Jhelum valley, 3500–4000 m., *Ludlow & Sherriff 7754* (BM, GH); Rajdhiangan Pass, 3500–4000 m., *R. R. Stewart 17974* (GH, MICH, US), *22556b* (GH), *19292* (GH); Tragbal, 3300 m., *R. R. Stewart 4800* (MICH), *Koelz 9167* (GH); Poonch, near Bantara Gali, 2700 m., *R. R. Stewart & Nasir 24084* (BM); above Gulmarg, *R. R. Stewart 10419, 8752* (GH); Haramukh, *Ludlow & Sherriff 7870* (GH). Miscellaneous: Herb. East Ind. Co., *Falconer s.n.* (K); *Kohli 21*(K).

6. **P. drummondii** Kazmi, sp. nov.

TYPE: Kashmir: Pir Panjal (south side), 11,000 ft., June 27, 1902, *Mr. J. R. Drummond 13919* (E-holotype).

Herba perennis, rhizomatibus horizontalibus subterraneis. Surculi emergentes simplices, erecti vel suberecti, ad 20 cm. alti, dense vel laxe pilis albis, plus minusve crispatis, patentibus, ad 1 mm. longis vestiti. Folia basalia et inferiora petiolata, petioli 10–20 mm. longi, alati, hirsuti, ad basim dilatati, lamina ad 45 mm. longa et 15 mm. lata, late lanceolata, obtusa vel subacuta, supra infraque pilis albis ad 1 mm. longis, plerumque patentibus vel subappressis vestita; folia caulina mediana et superiora ad folia inferiora similia, sessilia, sursum decrescentia. Inflorescentia terminalis, simplex vel bifurcata, 5–9-florae, in juventute brevis et scorpioidea, demum elongata; pedicelli desunt vel ad 1.5 mm. longi. Calyx ad basim divisus, lobi ad 5.5 mm. longi et 3 mm. lati, ovato-lanceolati, externe nervo primario et marginibus dense hirsutis, cetera laxe hirsuti; interne paene glaber, erectus. Corolla atrocaerulea ad purpurea, glabra, cylindrica, tubus 7–10 mm. longus, calycem excedens vel paene duplo longior; lobi ad 4 mm. longi et 3 mm. lati, ovati vel subrotundati, integri, interne subpuberuli, erecti vel subpatentes; appendices faucales triangulari-lingulatae, 2–3 mm. longae, 1–1.5 mm. latae ad basim, margines ciliati.

Antherae 1.5–2 mm. longae, oblongae, subsessiles vel filamenta ad 0.5 mm. longa, 3–6 mm. supra basim corollae inserta. Stylus 10 mm. longus, stigma capitatum. Fructus non visus.

DISTRIBUTION: West Pakistan, Kashmir.

West Pakistan: GILGIT AGENCY: Naltar, Sept. 1960, *McVean s.n.* (E).
Kashmir: Pir Panjal, 3600 m., *Drummond 13919* (E-type).

Only three species of the genus *Pseudomertensia* have faucal appendages, which are longer than broad, viz. *P. lindelofioides* (Rech. f. & Riedl) Riedl (in Rechinger, Fl. Iranica **48**: 61. 1967), *P. chitralensis* and *P. drummondii*. *P. lindelofioides*, which is distributed in eastern and northeastern Afghanistan and which can be expected in West Pakistan, is distinguished from the other two by having large calyces, 7–8 mm. long, corollas 14–15 mm. long, faucal appendages 3–4 mm. long and filaments 2–3 mm. long. In the other two species, along with the differences in form, the calyces do not exceed 6 mm., the corollas 12 mm., the faucal appendages 3 mm., and the filaments 2 mm. in length.

The new species *Pseudomertensia drummondii* is more closely related to *P. chitralensis* than *P. lindelofioides*. It is distinguished from *P. chitralensis* by having denser and longer, up to 1 mm. long, spreading trichomes on the stems and leaves. The trichomes in *P. chitralensis* are appressed and do not exceed 0.3 mm. in length, except for a few scattered ones on the stem and petioles. The leaves in *P. chitralensis* have much longer petioles, and ovate laminae which are roundish or obtuse at the apices, whereas the leaves of *P. drummondii* have shorter petioles and lanceolate laminae, which are obtuse or acutish at the apices. In texture, the leaves of *P. chitralensis* are thin, while those of *P. drummondii* are thick. Flowers of *P. drummondii* are subsessile or short pedicellate and the pedicels attain a maximum length of 1.5 mm., while the pedicels of *P. chitralensis* ordinarily reach a length of 4 mm. The calyx lobes of the former are ovate to ovate-lanceolate, while those of the latter are linear. Faucal appendages of *P. drummondii* are 2–3 mm. long, 1–1.5 mm. broad at base, triangular and ciliate at the margins, while those of *P. chitralensis* are 0.8–1.2 mm. long, 0.5 mm. broad at base, oblong-lingulate, narrowed in the middle and entire at the margins. The former has longer anthers and shorter filaments compared to those of *P. chitralensis*.

The specimen collected by McVean from Gilgit is a variation of *P. drummondii*. It agrees with the type specimen in all respects, except that it has slightly narrower calyx lobes, smaller corolla and the filaments are inserted only 3 mm. above the corolla base.

7. **P. chitralensis** (Riedl) Riedl in Rechinger, Fl. Iranica **48**: 62. 1967.

Mertensia chitralensis Riedl, in Køie & Rechinger, Biol. Skr. **13**(4): 228. 1963.

TYPE: Chitral: Runbur, 3200 m., *Bowes Lyon 664* (BM-holotype).
ICON.: Riedl, l. c., *fig. 174*. 1963, under *Mertensia chitralensis*.

Perennial with underground rhizomes. Emerging shoots simple or branched, ± 15 cm. tall, tender, clothed with thin, short, appressed trichomes. Basal leaves petiolate; petioles 1–8 cm. long, winged, membranous, ciliate below, clasping the shoots at the bases; lamina shorter than the petioles, elliptic, oblong-ovate or ovate-lanceolate, gradually attenuated towards the base, apex obtuse or roundish, rarely acute, margins entire, 2–5 cm. long, 0.8–1.7 cm. broad, uniformly covered on both surfaces with more or less loose, short, appressed trichomes; upper leaves few, smaller, and with shorter petioles. Inflorescence solitary, short, 2–3 cm. long when young, later elongated, 7–8 cm. long, bearing 7–12 flowers; pedicels 1–4 mm. long. Calyx divided to the base, lobes 4–4.5 mm. long, up to 0.7 mm. broad, in fruit elongated to 6 mm., linear, obtuse, erect, margins densely pubescent, trichomes up to 1 mm. long, few scattered trichomes on the upper surface. Corolla blue to bluish purple, infundibuliform, glabrous, 10–12 mm. long, tube 7–9 mm. long, slightly dilated upwards, lobes roundish, obliquely patent, ca. 2 mm. long and broad; faucal appendages 0.8–1.2 mm. long, 0.5 mm. broad, narrowed in the middle, slightly emarginate above. Anthers oblong, more or less rounded at both ends, ca. 1.2 mm. long, 0.4 mm. broad, tips approaching the sinuses between the corolla lobes; filaments 0.7 mm. long, slightly dilated at base, attached below the faucal appendages. Style filiform, ca. 11 mm. long; stigma capitate. Nutlets oblong or ovate, trigonous, 2.5–3 mm. long, ca. 1 mm. broad, slightly puberulous externally, pubescent inside, pallid.

DISTRIBUTION: West Pakistan.

West Pakistan: CHITRAL STATE: Rumbur, 3200 m., *Bowes Lyon 664* (BM); Pattisun, *Toppin 191* (K).

8. **P. anjumiae** Kazmi, sp. nov.[1]

TYPE: West Pakistan: Kurram, up the Shend Toi valley, near water at an elevation of 11,000 ft., *Aitchison 192* (BM-holotype, GH-isotype).

Surculi tenues subterranei, radices fibrosas emittentes fibroso-radicantes et squamis parvis obsiti. Caules floriferi ad 20 cm. longi, arcuati vel erecti tenues herbacei, pilis patulis sparse obsiti, in cincinnum singulum terminalem aphyllum abeuntes. Folia basalia plura, lamina oblongo-ovata vel oblanceolata, (1–)2–4(–5) cm. longa, 5–10 mm. lata, basi longe attenuata, apice breviter attenuata vel subrotundata, plana, integra, tenuissime molliterque herbacea, costa mediana tenuis, nervis secundariis vix visibilibus, supra et subtus pilis sparsis brevissimis appressis tecta, longe tenuiter petiolata, petiolo 2–5 cm. longo; folia caulina pauca breviter petiolata, petiolis 4 cm. longis, 0.5 mm. latis. Inflorescentiae solitariae, primo densae, scorpioideae demum ad 8 cm. elongatae, 5–20-florae. Pedicelli 1–10 mm. longi. Calyx 3–4 mm. longus ad basin usque in laciniis anguste linearibus obtusis fissus, pilis arcuatis patulis ad 1 mm. longis obsitus. Corolla quam calyx duplo longior, in sicco caeruleo-violacea, 8

[1] I named this species after the name of my wife, Anjum.

mm. longa, subcylindrica vel infundibuliformis, utrinque glabra, lobis erectis vel oblique patulis, ca. 1.5 mm. longis et latis, rotundatis. Fornices tenuiter evoluti. Filamenta 1–1.2 mm. longa, 7 mm. supra basin tubi affixa. Antherae ca. 1 mm. longae versatiles, atrae, oblongae, ad apicem et basin rotundatae. Stylus corollam saepe superans, tenuiter filiformis, pallidus. Stigma minutum subcapitatum. Nuculae ignotae.

DISTRIBUTION: West Pakistan.

West Pakistan: KURRAM: Shend Toi valley, *Aitchison 192* (BM, GH).

The specimen cited here, collected by Aitchison from Kurram valley, has been cited by Riedl (in Rechinger, Fl. Iranica **48**: 62. 1967) under *Pseudomertensia echioides*. On close examination it was found to be very different from that species and to be worthy of recognition. The important distinguishing characters of *P. echioides* are the very short (0.5 mm.) filaments, shorter than the anthers (1.5–1.9 mm.) which are acute at their apices, and the absence of faucal appendages. These characters are well correlated with the long (3–4.5 mm.) and narrow (1.5 mm.) corolla lobes, which more or less equal or sometimes even exceed the corolla tube in length. *Pseudomertensia anjumiae* differs from *P. echioides* in having longer (1–1.2 mm.) filaments, equalling or slightly exceeding the length (1 mm.) of the anthers which are roundish at apices. The faucal appendages are quite developed. Corolla lobes are much reduced, only 1.5 mm. long and broad, about 1/5 the length of the corolla tube, and not oblong-ovate but roundish. *Pseudomertensia anjumiae* is distinguished from the related species, *P. moltkioides*, in having shorter corolla lobes and longer filaments. In *P. moltkioides* corolla lobes are 2.5–4.5 mm. long, 2–3 mm. broad, and oblong-ovate in shape; the filaments, 0–0.5 mm. long, are dilated at the base.

9. **P. nemorosa** (DC.) Stewart & Kazmi, comb. nov.

Lithospermum ovalifolium Decne. in Jacquem. Voy. Inde Bot. 121. 1844.
Eritrichium nemorosum A. DC. in DC. Prodr. **10**: 123. 1846.
Mertensia nemorosa (DC.) I. M. Johnston, Jour. Arnold Arb. **37**: 305. 1956.
Mertensia moltkioides (Benth.) C. B. Clarke var. *thomsoni* C. B. Clarke in Hook. f. Fl. Brit. India **4**: 170. 1883, *syn. nov.*

TYPE: Kashmir: In humidis nemorum ad Ouri, May 4, 1831, *Jacquemont s.n.* (GH, P).

ICON.: Jacquemont, l. c. *t. 124*. 1844, under *Lithospermum ovalifolium*; Coventry, Wild Fl. Kashmir **3**: *t. 44*. 1930, under *Mertensia moltkioides*.

Perennial with stout, little branched, underground rhizomes, up to 20 cm. long, sometimes to 10 mm. thick. Emerging shoots weak, curved or erect, 6–15(–20) cm. tall, clothed mostly with spreading, thin, white trichomes up to 1 mm. long. Basal leaves petiolate; petioles 2–8 cm. long, hairy, broad and clasping the shoot at their bases; lamina ovate, elliptic, or ovate-lanceolate, margins entire, mostly acute at apex, round or ob-

tuse at base, rarely truncate, never cordate, (2–)3–7(–8) cm. long, 1–4.5 cm. broad, upper surface slightly hairy, lower surface comparatively densely hairy especially on nerves, trichomes thin, not arising from tuberculate bases, appressed to suberect, rarely patent; upper cauline leaves shorter, narrower, with short petioles, subsessile or sessile. Inflorescence at flowering 4–9 cm. long, bearing 6–14 flowers, in fruit much elongated, with fruits sometimes up to 10 mm. distant; pedicels 1–9 mm. long, hairy. Calyx divided to the base, lobes linear-oblong, obtusish, erect, up to 7 mm. long, covered externally with subappressed or spreading trichomes. Corolla blue, bluish-purple to deep blue, glabrous, corolla tube cylindrical, (8–)9–11 mm. long, lobes ovate, suberect to patent, 3.5–4 mm. long, 3–3.5 mm. broad at the base; faucal appendages small 0.7–0.8 mm. broad, 0.5–0.6 mm. long, anthers 1 mm. long, 0.5 mm. broad, oblong, rounded at both ends. Filaments very short, nearly triangular, 0.5 mm. high, 0.7 mm. broad at the dilated base, attached in between and slightly below the bases of the faucal appendages. Style filiform, ca. 8 mm. long; stigma small, subcapitate. Nutlets 3 mm. long, 1.5 mm. broad, acute at apices, slightly verruculose on the ridges, dark brown.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: HAZARA DIST.: Kaghan valley, between Naran and Batakundi, *Kazmi 795a* (PES); SWAT STATE: Mt. Ilam, *R. R. Stewart 24373* (RAW); Miscellaneous: locality unknown (probably from Swat) *Kazmi s.n.* (PES).

Kashmir: Poonch: Serimang, 2000–2700 m., *R. R. Stewart & Nasir 25540* (BM); Lidder valley: Kolhoi, *Inayat 25711* (K); 3300 m., *Ludlow 8* (BM); Chashma Shai, 2300 m., *R. R. Stewart 10926* (GH); above Uri on Poonch road, 2000 m., *R. R. Stewart 12954* (GH); ad Ouri (Uri ca. 20 miles from Baramula and 40 miles west of Srinagar), *Jacquemont s.n.* (GH, P); Lidderwat, 3000 m., *Coventry 575* (K), *Evershad s.n.* (BM); Sind valley, Gangangir, 2500 m., *Rich 1075* (K); Kishanganga valley: near Nilam, *Kazmi s.n.* (PES); Islampur, *Kazmi 295b* (PES); Kel, *Kazmi s.n.* (PES); between Shardi and Kel, 1950–2100 m., *Schmid 1744* (BM, MICH); Sind valley, Mehanmarg, 2500 m., *Ludlow & Sherriff 8147* (BM); Chenab-Ravi watershed, Badawar to Padri Pass, June 3, 1848, *Thomson s.n.* (K); south of Chenab valley between Baleta and Katti, Herb. Ind. Or. Hook. f. & Thoms., May 14, 1948, *Thomson s.n.* (K). Miscellaneous: Hab. Himal. Occ., 6000–7000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH); Herb. East India Co., *Falconer s.n.* (GH); *Palmer s.n.* (BM).

Pseudomertensia nemorosa is very closely related to *Mertensia racemosa* (Royle) C. B. Clarke (in Hook. f. Fl. Brit. India **4**: 171. 1883) of Kumaon, Bashahar and Kulu, which also agrees more closely in its characters to *Pseudomertensia* than to *Mertensia* and is here recombined as *Pseudomertensia racemosa* (Royle) Kazmi.[2] *Pseudomertensia nemorosa* differs from *P. racemosa* in its blue-purple rather than white corollas, its more pubescent leaves, not subcordate at the bases, and its coarser

[2] **Pseudomertensia racemosa** (Royle) Kazmi, comb. nov.
Myosotis racemosa Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1839.
Mertensia racemosa (Royle) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 171. 1883.

habit. The next most closely related species is *P. moltkioides* from which it differs mainly in the form and size of leaves. In *P. moltkioides* the leaves are oblong, oblong-lanceolate, lanceolate, or rarely narrowly lanceolate and are up to 10(–12) mm. broad, their bases always attenuated into short or long petioles; while in *P. nemorosa* the leaves are ovate, elliptic, or ovate-lanceolate, and are usually 10–45 mm. broad, their bases always round, obtuse or rarely truncate, and not gradually attenuated into petioles as in *P. moltkioides*.

Dr. R. R. Stewart has compared the specimens, *Inayat 25711* and *Rich 1075* at the Kew Herbarium with Thomson's collection from Islamabad, Kashmir, on which *Mertensia moltkioides* var. *thomsoni* C. B. Clarke (in Hook. f. Fl. Brit. India **4**: 170. 1883) is based, and found them to be identical. These specimens (cited above) and Clarke's description "Radical leaves 3 × 1 1/2 in. (75 mm. long, 40 mm. broad), base subobtuse" agree with *P. nemorosa*.

10. **P. moltkioides** (Royle ex Benth.) Kazmi, comb. nov.

Myosotis moltkioides Royle ex Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1836; *t. 73. fig. 1.* [Dec.] 1835.
Anchusa moltkioides Royle ex Benth. *l. c.*; DC. Prodr. **10**: 51. 1846.
Lithospermum moltkioides (Royle ex Benth.) Decne. in Jacquem. Voy. Inde Bot. 122. 1844.
Mertensia tibetica C. B. Clarke in Hook. f. Fl. Brit. India **4**: 171. 1883.
Mertensia nuristanica Rech. f. Ann. Naturh. Mus. Wien **58**: 56. 1951.

TYPE: Kashmir: Pirpenjal, *Royle* (?)

ICON.: Royle, *l. c.* 1835, under *Anchusa moltkioides*.

Perennial with long, slender, branched, underground rhizomes, up to 5 mm. thick. Emerging shoots profusely leafy at the bases, naked or with few distant leaves above, 5–15 cm. tall, clothed usually with short and appressed or sometimes with long and patent trichomes. Basal leaves petiolate, petioles shorter or longer than lamina, lamina oblong to oblong-lanceolate to lanceolate, rarely linear-lanceolate, entire, acute to obtuse, (including petioles) 15–70(–80) mm. long, 2–10(–12) mm. broad, covered on both surfaces with short appressed to subappressed trichomes, rarely glabrous below, cauline leaves few, sessile, shorter and narrower than the basal ones. Inflorescence 2–3 cm. long with sessile or subsessile closely set flowers when young, later elongated up to 7 cm. long, with distant (up to 10 mm. apart), short pedicellate flowers; pedicels up to 3 mm. long. Calyx divided to the base, lobes linear to linear-lanceolate, obtuse to acute, erect, 3–4(–5) mm. long, 0.5 mm. broad, covered with short, patent to subpatent trichomes. Corolla blue, bluish-purple to deep bluish-purple, infundibuliform, externally glabrous, internally glabrous to puberulous or minutely pubescent above the throat, tube 8–15 mm. long, lobes oblong-ovate, patent, 2.5–4.5 mm. long, 2–3 mm. broad; faucal appendages well developed, broader than long, slightly emarginate and puberulous. Anthers oblong, roundish at both ends, 1–1.75 mm. long;

filaments more or less broad at the base, 0–0.5 mm. long. Style filiform; stigma subcapitate. Nutlets ovate, trigonous, light to dark brown, 3 mm. long.

DISTRIBUTION OF SPECIES: Afghanistan, West Pakistan, Kashmir, northwest India, and Tibet.

This species, *Pseudomertensia moltkioides*, is very variable in the length of petioles and lamina, number of leaves on the shoots, length of calyx lobes and corolla tube, indument of minute trichomes on the corolla throat, and the insertion of the anthers on the corolla. The four varieties which follow may easily be distinguished from one another.

KEY TO THE VARIETIES

a. Anthers distinctly below the bases of the faucal appendages. ..... 10a. var. *moltkioides*.
a. Anthers distinctly exceeding or surpassing the bases of the faucal appendages.
  b. Leaves linear-spathulate. ..... 10d. var. *tanneri*.
  b. Leaves oblong to oblong-lanceolate.
    c. Leaves short petiolate, scapes naked, corolla internally, above the throat, puberulous. ..... 10b. var. *primuloides*.
    c. Leaves with long petioles, scapes leafy, corolla internally, above the throat, densely minutely pubescent. ..... 10c. var. *leichtlinii*.

10a. Var. moltkioides.

Basal leaves usually with long, rarely with short petioles; corolla tube mostly 3–5 times longer than the calyx; corolla usually glabrous within, rarely puberulous; anther tips just below to a few millimeters below the faucal appendages.

West Pakistan: CHITRAL STATE: Golen, Shishikuh, 4700 m., *Bowes Lyon 106* (BM). GILGIT AGENCY: Rama valley, southwest of Astore, 4000 m., *Lankester & Pearson 1402, 1342* (BM); upper end of Hushe valley, Chogolisa glacier basin, *Webster 6241* (GH), *Humphrey & Sufi s.n.* (MICH); at the foot of Masherbrum, *Webster & Nasir 6202* (GH); Astor, Alampila, *Duthie 1217* (BM, K); Kamri top, 4000 m., *R. R. Stewart 18675* (GH); Mekerum, Hispar glacier, 3500 m., *Russell 1450* (GH); Haramosh La, *Culbert 86* (BM); Agres Camp, below Hispar Pass, Karakorum, 4100 m., *Conway 209* (BM); near Hispar, Shukurri, 4400 m., *Conway 166* (K); Nagar, Gharesa glacier, slope facing north, 12 miles east of Nagar, *Polunin 6127* (BM); Minapin glacier, 4100 m., *Lloyd & Megan 105* (BM). HAZARA DIST.: Kaghan valley, between Naran and Saiful Maluk, ca. 2700 m., *Kazmi 200b* (PES); Ganji Pahari, near Naran, half way to the top, ca. 2500 m., *Kazmi 852c* (PES); 1.5 miles north of Naran, *Burtt & Arshad Ali B857* (E); Basal, *Schmid 363* (E); between Shahid Pani and Musa ka Musalah, on rocky slope facing Kaghan valley, ca. 3000 m., *Kazmi 2514* (PES); Siran valley, near the foot of Musa ka Musalah, ca. 2800 m., *Kazmi 2491* (PES).

Kashmir: Apharwat above Gulmarg, 4000 m., *Rich 1230* (K); Apharwat, 4400 m., *Polunin 56/196* (E); above Gulmarg, *Fuller 153* (K); Pirpanjal, *Inayat 25707* (K); top of Masjid Gali, 4500 m., *R. R. Stewart 18363* (GH,

MICH); Kishtwar, Dudhari Pass, 4000 m., *Ludlow & Sherriff 9216* (GH); Kishanganga valley, above Nilam, ca. 3200 m., *Kazmi 302c* (PES); Chinari, Zakia Bandi, on rocky slopes, *Kazmi 258a* (PES).

The binomial *Mertensia moltkioides* (Benth. in Royle) C. B. Clarke (in Hook. f. Fl. Brit. India **4**: 170. 1883) is based on the illustration of *Anchusa moltkioides* (Royle ex Benth. in Royle, l. c. *t. 73. fig. 1.* 1835), described by Royle ex Bentham (in Royle, *l. c.* **1**: 305. 1836) as *Myosotis moltkioides*, is a misidentification which was further confused by C. B. Clarke's description (*l. c.*) and, therefore, ignored by many authors.

The illustration of *Anchusa moltkioides* gives all the necessary details of the form of the leaves and the structure of flowers and should be accepted as type.

This illustration shows clearly the scapose peduncle, oblong leaves with long petioles, and the anthers distinctly below the faucal appendages. On the basis of these distinguishing characters two of the three specimens cited by C. B. Clarke (*l. c.*) (Kashmir, *Falconer*, and near Islamabad, *Thomson*) do not agree with *M. moltkioides*, but are, rather, *Pseudomertensia nemorosa*. The collection of Dr. Watt from Pangee, which I was unable to examine, may also not belong to *Mertensia moltkioides*.

Actually C. B. Clarke's description of *Mertensia tibetica* represents the type of *Pseudomertensia moltkioides*. He cited the following details "— leaves small subradical long-petioled elliptic, peduncles long subscapose — anthers entirely below the scales — nutlets as of *M. moltkioides*." *Pseudomertensia nuristanica* Rech. f. represents only a form of *P. moltkioides* in which the anthers are attached to the corolla tube a few millimeters below the faucal appendages. Both these binomials are therefore synonyms of *P. moltkioides*.

Riedl (in Rechinger, Fl. Iranica *l. c.*) recognized the specific name *Pseudomertensia primuloides* for the taxon containing the forms of *Mertensia tibetica* and *M. nuristanica*. As the dates of publication of Royle's Illustr. (*l. c.* 1835, 1836) precede the date of publication of Jacquemont's *Voyage* (*l. c.* 1844), *P. moltkioides* has priority.

10b. Var. **primuloides** (Decne.) Kazmi, comb. nov.

Eritrichium primuloides Decne. in Jacquem. Voy. Inde Bot. 123. 1844; DC. Prodr. **10**: 125. 1846.

Mertensia primuloides (Decne.) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 171. 1883, excl. var.

Pseudomertensia primuloides (Decne.) Riedl in Rechinger, Fl. Iranica **48**: 62. 1967, *pro parte*.

TYPE: Kashmir: Pirpenjal, *Jacquemont s.n.* (P).

ICON.: Jacquemont, l. c. *t. 128.* 1843.

Basal leaves usually with short, sometimes with long petioles; corolla tube usually 2 to 3 times longer than the calyx; corolla internally, above the throat, usually puberulous, sometimes minutely pubescent; anthers distinctly exceeding or surpassing the bases of faucal appendages.

West Pakistan: CHITRAL STATE: Drosh Nullah, 3800 m., *Toppin 757* (K); Shera Shing Pass, 4800 m., *Stainton 3208* (BM); Ziarat (Lowari Pass), 3000 m., *Stainton 3208* (BM), *2330* (E). HAZARA DIST.: Kaghan valley, *Champion s.n.* (GH); Makra, 4500 m., *Duthie s.n.* (K); between Shogran and Bhunja, *Kazmi 732b* (PES); near Sari, between Shogran and Makra, ca. 3000 m., *Kazmi 2212b* (PES); Chapri, 28. 7. 1899, *Inayat s.n.* (K); Naran, stony ground, 3000 m., *Jafri & Ali 3389*, *3332* (E); Naran, June 1960, *McVean s.n.* (E). Miscellaneous: northwest India (marked b), *J. L. Stewart s.n.* (E).

Kashmir: Apharwat, above Gulmarg, 3400 m., *Pinfeld 193* (BM), *Rich 1257* (K), *R. R. Stewart 15486*, *10327*, *8604* (GH), *Steane 43* (E); above Gulmarg, *Aitchison 73* (K); Pirpanjal, 10. 8. 1901, *Inayat s.n.* (K); Bringhi valley, Mantnar Nullah, 4300 m., *Ludlow & Sherriff 8050* (BM, GH); Mantnar valley, near Desu, 4100 m., *Ludlow 115* (GH); Kishenganga valley, near Nilam, *Kazmi 316b* (PES); Muzafarabad, Musa, 18. 7. 1899, *Inayat s.n.* (K); Kamri Pass, 4500 m., *Duthie 12576* (BM); Kamri Pass top, 4300–4600 m., *R. R. Stewart 22690* (GH); Ablau valley, Bringhi river, 4000–4300 m., *Ludlow 21* (BM).

Among the specimens cited above, *Ludlow 21* differs from the others in having filaments up to 0.5 mm. long.

10c. Var. **leichtlinii** Kazmi, var. nov.

TYPE: Hazara, *Max Leichtlin 4* (BM).

Folia basalia longipetiolata, petiolis saepe laminis aequantibus; corolla intra, supra appendices fauces, minute densique pubescens; scapi plerumque foliati.

West Pakistan: HAZARA DIST.: *Duthie s.n.* (K); *Leichtlin 4* (BM-holotype of var.); between Balaket and Babusar Pass, *Abel 132* (BM); Kaghan valley, Naran, *Shaukat Ali 125* (BM).

10d. Var. **tanneri** (C. B. Clarke) Stewart & Kazmi, comb. nov.

Mertensia primuloides (Decne.) C. B. Clarke var. *tanneri* C. B. Clarke in Hook. f. Fl. Brit. India **4**: 171. 1883.

TYPE: Daskin, Astore, *Tanner 10* (K).

ICON.: Riedl, in Køie & Rechinger, Biol. Skr. 13(4): *fig. 125*. 1963.

Leaves linear-spathulate with longer petioles, calyx lobes 4–5 mm. long; corolla violet, corolla tube ca. 8 mm. long.

West Pakistan: GILGIT AGENCY: Daskin, Astore, *Tanner 10* (K); Sai, Gilgit, *Tanner s.n.* (K); Rattu et Goriket, *Schmid 1774* (BM); Rama valley, southwest of Astore, 3500 m., *Lankester & Pearson 2030* (BM). HAZARA DIST.: Kaghan valley, Naran, *Barrett s.n.* (K).

9. **Anoplocaryum** Ledeb. Fl. Rossica 3: 154. 1847.

Echinospermum sect. 3. *Anoplocaryum* Turcz. in Bull. Soc. Nat. Moscou **23**(1): 522. 1850.

TYPE SPECIES: *Anoplocaryum compressum* (Turcz.) Ledeb.

Annual (or perennial ?) herbs. Basal leaves usually petiolate. Inflorescence bracteate, pedicellate, pedicels usually longer than the calyx and reflexed in fruit. Calyx divided to the base, not much enlarged in fruit. Corolla hypocrateriform to subrotate; faucal appendages distinct. Gynobase shortly pyramidal with 4 triangular depressions. Nutlets ovoid, rough or slightly tuberculate, margins irregularly setulose, carinate internally from the carunculate scar to the top.

Species about 5, distributed from China to the Western Himalayas.

A. brandisii Brand, Repert. Sp. Nov. **22**: 100. 1925, Pflanzenr. IV. **252**(Heft 97): 116. 1931.

TYPE: Chamba State: Sach Pangi, *Brandis 3166* (DD); Lahul, *Brandis 3236* (DD); Haelle (?), *Brandis 3996* (DD), holotype not indicated.

Perennial or annual herb. Stems many, slender, thinly covered with short, thin, appressed trichomes, 15–30 cm. tall. Basal leaves 15–25 mm. long, 2–4 mm. broad, entire, obtuse, gradually narrowed at the base into a short petiole, covered with thin, short, appressed trichomes on both surfaces; cauline leaves subsessile to sessile, shorter and narrower. Inflorescence terminal, lax, lower flowers bracteate; pedicels hairy, 1–2 mm. long, elongated in fruit, to 12 mm., recurved. Calyx divided to the base, lobes lanceolate, slightly hairy, in flower 1.5 mm. long, in fruit usually subreflexed, to 2.5 mm. long, 0.5 mm. broad. Corolla subrotate, 4–5 mm. in diameter; faucal appendages semilunar. Gynobase triangular, distinct from the equally long style. Nutlets 3–4, ovoid, 2 mm. long, margins densely minutely setulose, granulate and slightly rugose on both surfaces, internally distinctly and externally slightly carinate, attached obliquely to the gynobase by a large carunculate scar.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: GILGIT AGENCY: Niltar valley, north of Gilgit, 3500–3700 m., *Duthie 12425* (GH, K). Reported from near Gilgit, *Roberts* (Brand, *l. c.*).

10. **Eritrichium** Schrad. Comment. **4**: 186. 1820.

Eritrichium Schrad. sect. *Eu-eritrichium* DC. Prodr. **10**: 124. 1846.

TYPE SPECIES: *E. nanum* (Vill.) Schrad.

Annual or perennial, strigose or villous herbs with alternate leaves. Racemes simple or branched, usually terminal or sometimes axillary. Calyx divided to the base, lobes 5, sometimes enlarged and reflexed in fruit. Corolla subrotate to infundibuliform, lobes spreading; faucal appendages distinct. Stamens inserted on the corolla tube, included; anthers ovate. Ovary 4-lobed, style filiform, stigma capitate. Gynobase subprismatic-pyramidal, shorter than the style. Nutlets 4, surpassing the gynobase, attached obliquely to the depressions in the gynobase, at margins usually appendiculate; appendages various.

Species about 25, centering in Asia, distributed to Europe and America.

KEY TO THE SPECIES

a. Basal leaves in rosettes, sessile, covered on both surfaces with trichomes 1–2 mm. long, margins ciliate. ..... 1. *E. nanum.*
a. Basal leaves not in rosettes, petiolate, covered on both surfaces with trichomes up to 1 mm. long, margins usually not ciliate, rarely with a few scattered long trichomes.
  b. Cauline leaves gradually narrowed towards the bases, subsessile to short petiolate. ..... 2. *E. fruticulosum.*
  b. Cauline leaves broad at the bases, always sessile.
    c. Cauline leaves ovate to oblong-ovate, roundish to obtuse at apices, usually covered with unequal trichomes. ..... 3. *E. spathulatum.*
    c. Cauline leaves oblong-lanceolate to linear-filiform, apices obtuse to acute, usually covered with equal trichomes.
      d. Nutlets triangular-oblong (excluding appendages), 1.5 mm. long, 1 mm. broad, outer surface convex or slightly longitudinally raised in the middle, marginal appendages 0.2 mm. long, distant, not confluent at their bases. ..... 4. *E. patens.*
      d. Nutlets ovate (excluding appendages), 2 mm. long, 1.5 mm. broad, outer surface plane or slightly concave, marginal appendages 1 mm. long, confluent at their bases. ..... 5. *E. canum.*

1. **E. nanum** (Vill.) Schrad. Comment. Soc. Regiae Sci. Gott. **4**: 186. 1820; M. Pop. in Fl. URSS. **19**: 514. 1953; Riedl in Rechinger, Fl. Iranica **48**: 64. 1967.

Myosotis nana Vill. Hist. Pl. Dauph. **2**: 459. 1878, Prosp. Pl. Dauph. 21. 1879.

TYPE: "Sur les sommets des Alpes au dessus de Brande et d'Allemont . . .," without citation of collector's name (?).

ICON.: Vill. l. c. *t. 13.* 1878; Hegi, Ill. Fl. Mitt.-Eur. **5**(3): *t. 219, fig. 2a–c,* & *fig. 3095.* 1927.

Perennial, densely caespitose; roots much branched near the surface of the ground, each branch bearing a thick rosette of leaves and producing a single, usually simple or rarely branched stem. Stems very short, to 12 cm. long, covered thinly or densely with thin, silky, usually spreading trichomes. Basal leaves numerous, sessile, oblong-lanceolate, entire, roundish or obtuse at apices, margins thickly ciliate, 5–10 mm. long, 2–3(–5) mm. broad, both surfaces covered with thin, silky, trichomes up to 2 mm. long; cauline leaves few, usually narrower. Inflorescence short, 3–6-flowered, lower flowers bracteate, bracts leaflike, 1–2 mm. long; upper flowers subsessile, lower flowers pedicellate, pedicels up to 1.5 mm. long, hairy. Calyx divided nearly to the base, lobes oblong-lanceolate, in flower 2.5–3 mm. long, in fruit elongated to 4 mm., densely hairy, trichomes long, sometimes yellowish. Corolla usually blue, rarely white, with a yellow eye, campanulate-rotate, tube equalling or a little longer than the calyx, slightly narrowed at the throat, lobes ovate, spreading,

0.5–3.5 mm. long, 1–3 mm. broad; faucal appendages linear-horizontal. Nutlets ca. 2.5 mm. long, at margins dentate, glabrous.

DISTRIBUTION OF SPECIES: European Alps, Caucasus, Altai, Siberia, western China, Tibet, Afghanistan, West Pakistan, Kashmir, northwestern India.

1a. Subsp. **nanum.**

Basal leaves many; stems short; corolla 6–7 mm. long.

DISTRIBUTION OF SUBSP.: Represents the species in the European and western Asian portions of its range.

1b. Subsp. **villosum** (Ledeb.) Brand, Pflanzenr. IV. 252(Heft 97): 189. 1931; Riedl in Rechinger, Fl. Iranica **48**: 64. 1967.

Myosotis villosa Ledeb. Mem. Acad. St.-Pétersb. **5**: 516. 1815; Flora Altaica **1**: 191. 1829.

Eritrichium villosum (Ledeb.) Bunge, Verzeichn. Altaigebirg. Pflanzen 14. 1836; DC. Prodr. **10**: 126. 1846.

Echinospermum sericeum Benth. in Royle, Illustr. Bot. Himal. Mount. 306. 1836.

Eritrichium sericeum (Benth. in Royle) DC. Prodr. **10**: 126. 1846.

Eritrichium basifixum C. B. Clarke in Hook. f. Fl. Brit. India **4**: 165. 1883.

E. nanum subsp. *villosum* var. *eu-villosum* Brand, l. c. 190. 1931.

TYPE: "Habitat in Sibiriae alpibus," without citation of collector's name (LE).

ICON.: Ledeb. Icon. Fl. Rossica **2**: *t. 215*. 1830.

Basal leaves few, stems longer than in the typical subsp.; corolla 3–5.5 mm. long.

DISTRIBUTION OF SUBSP.: Altai, Siberia, Tibet, Afghanistan, West Pakistan, Kashmir, and northwest India.

West Pakistan: GILGIT AGENCY: Rimochagma valley 4700 m., 20. 7. 1892, *Duthie s.n.* (BM, E); Baltistan, *Hunter-Weston 10253* (MICH); snow field on the south slope of Burja La, 4700–5000 m., *Webster & Nazir 6546* (GH); Talala, 4300 m., *Koelz 9747* (GH), *R. R. Stewart 20770* (GH); Jutial Nullah, *R. R. Stewart 26326* (BM); Ramna valley, southwest of Astore, 4000 m., *Lankester & Pearson 1345, 1346* (BM); Chota Deosai, 4000–4500 m., *R. R. Stewart 19934* (GH, MICH, US). HAZARA DIST.: Kaghan valley, between Paya and Makra, above Shogran, ca. 3000 m., *Kazmi 2144b* (PES); Gitidas, 3700 m., *Metz s.n.* (MICH); Kaghan valley, *I. I. Chaudhri s.n.* (RAW); Siran valley, near Shahid Pani, ca. 3100 m., *Kazmi 193c* (PES).

Kashmir: Kamri Pass top, 4500 m., *R. R. & I. D. Stewart 18708, 22677* (GH); Burzil Pass, 4300 m., *Duthie 14038* (BM); Zaskar, Pansi La, 5500 m., *Koelz 5938* (GH, MICH, US); Kargia, Lagong, 4500 m., *Koelz 5392* (GH, MICH, US); Ladak, Hanu Yogma via Handamir up the Cherbat La Pass (Pass between Indus valley and the Shayok valley), *Schlagintweit 6513* (GH); Barnaj Nullah, Sap-

phire mines, Kishtwar, *Ludlow & Sherriff 9151* (GH); Masjid Gali top, 4000 m., *R. R. & I. D. Stewart 18363B* (GH).

2. **E. fruticulosum** Klotzsch, Reis. Prinz Wald. Bot. 96. 1862.

E. strictum Decne. in Jacquem. var. *fruticulosum* (Klotzsch) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 164. 1883.

TYPE: Himalaya, *Dr. Hoffmeister s.n.* (HEID).

ICON.: Klotzsch, l. c. *t. 62*. 1862.

Perennial herb with woody tap root up to 15 cm. long. Stems many, erect to decumbent, slender, up to 30 cm. long, simple or sometimes branched in the upper part; branches short, stem and branches green, covered with thin, white, antrorsely appressed or subappressed soft trichomes not exceeding 0.5 mm. in length. Basal leaves few, petiolate, petioles slender, hairy, up to 20 mm. long; lamina pale green, ovate-lanceolate, ca. 25 mm. long, 5 mm. broad, obtuse, attenuate towards the base, covered uniformly and loosely on both surfaces with thin, appressed trichomes up to 0.5 mm. long; cauline leaves subsessile to short petiolate, petioles sometimes up to 3 mm. long, lamina as in the basal leaves, acutish, shorter and narrower. Inflorescence simple or rarely geminate, racemes loose, 10–15-flowered, bracteate; pedicels slender, hairy, more or less reflexed in fruit, up to 6 mm. long. Calyx divided to the base, lobes 1–1.5 mm. long, 0.2–0.3 mm. broad in flower, lanceolate, narrower towards the base, pubescent on both faces, enlarged in fruit to 2.5 mm. long and 0.7 mm. broad, spreading or slightly reflexed. Corolla light blue with a yellow eye, rotate, tube more or less equalling the calyx, lobes roundish, 1.5 mm. long and broad. Nutlets 4, excluding glochidiate appendages, 1.7–2 mm. long, 0.8–1 mm. broad, roundish at the base, acutish at apex, outer face convex, margined with glochidiate non-confluent appendages, 0.5 mm. long, 0.2 mm. broad at base, pubescent on both faces with short, stiff, erect trichomes.

DISTRIBUTION: West Pakistan, Kashmir, northwest India.

West Pakistan: GILGIT AGENCY: Gilgit proper, Manugah Nala, river bank, 3500 m., *J. W. Thornley 27* (BM); Baltistan, Shagurthang valley, 3000–3500 m., *Duthie 12144* (BM); Hunza, near Baltit, 3000 m., *R. R. Stewart 26327* (BM). QUETTA DIST.: Ziarat, 2600 m., 10. 9. 1887, *Lace s.n.* (E).

Kashmir: Ladakh, Gya, *Koelz 6412* (MICH, US); Nubra, Tsanglung Pass to Murzetau, 31. 7. 1856, *Schlagintweit s.n.* (GH); Rupshu, 4700 m., *Koelz 6654* (MICH, US). Miscellaneous: Himal. Bor. Occ., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM, GH).

C. B. Clarke (*l. c.*) recognizes *Eritrichium fruticulosum* as a variety of *E. strictum* and distinguishes it from *E. strictum* and its variety *thomsoni* by "weaker, greener, stems diffuse sometimes with divaricate branches." *Eritrichium strictum* and its variety *thomsoni* are considered in this work as synonyms of *E. canum* from which *E. fruticulosum* differs not only in

being more herbaceous with slender and more or less decumbent stems, but also in the form and pubescence of the leaves, and the shape and appendages of the nutlets.

The figure given by Klotzsch (*l. c.*), which should be accepted as the type, shows very clearly the sessile or short petiolate cauline leaves narrowed towards the base, generally thinly and uniformly covered with very short appressed trichomes. These characters together with the oblong form of the nutlets, which are roundish at the base and acutish at apex, margined with non-confluent appendages 0.5 mm. long, 0.2 mm. broad at the base and with both surfaces covered with short, stiff, erect trichomes, distinguish this species from its close relatives. In *E. canum* and its varieties the leaves are densely pubescent and are not gradually attenuated towards the base, but are broad and sessile. The nutlets are larger, with longer appendages, confluent at base and forming narrow or broad marginal wings.

3. **E. spathulatum** (Benth. in Royle) C. B. Clarke in Hook. f. Fl. Brit. India **4**: 164. 1883.

Echinospermum spathulatum Benth. in Royle Illustr. Bot. Himal. Mount. 306. 1836; DC. Prodr. **10**: 142. 1846.

Eritrichium jacquemontii Decne. in Jacquem. Voy. Inde Bot. 122. *t. 127*. 1843.

E. rupestre (Pall.) Bunge var. *pectinatum* (Pall.) Brand subvar. *spathulatum* (Benth. in Royle) Brand, Pflanzenr. IV. **252**(Heft 97): 193. 1931.

TYPE: Chango in Kunawur, with citation of collector's name (K, P).

ICON.: Jacquemont, l. c. *t. 127*. 1843, as *Eritrichium jacquemontii*.

Perennial, weak, decumbent herb. Stems many, to 20 cm. long, simple or branched, greenish, covered thinly or densely with short, appressed, white trichomes. Basal leaves petiolate, petioles 10–20 mm. long, slender, hairy; lamina, ovate-lanceolate, 20–30 mm. long, 3–7 mm. broad, gradually attenuated towards the petiole, obtuse to roundish at apex, margins entire, both surfaces covered thinly or densely, usually with unequal, subpatent white trichomes sometimes arising from tuberculate bases, up to 0.5 mm. long or even longer at the margins; cauline leaves sessile, oblong-ovate to ovate, gradually becoming reduced in size upwards, indument similar to that of basal leaves. Inflorescence usually branched, up to 20 mm. long, hairy, many flowered, bracteate, bracts ovate; pedicels slender, hairy, in flower up to 2 mm. long, in fruit to 6 mm. long, erect. Calyx divided to the base, lobes oblong-ovate, 1.5 mm. long, 0.5 mm. broad, usually densely hairy with longer trichomes at the margins, erect, in fruit slightly enlarged and sometimes reflexed. Corolla sky blue with a broad yellowish eye, 3–4 mm. long, rotate-campanulate, tube more or less equalling the calyx, lobes 2–2.5 mm. long, roundish, patent. Nutlets 2–3.5 mm. long, 1.3–2.5 mm. broad, glabrous or minutely hairy on both surfaces, margins appendiculate, appendages up to 0.6 mm. long,

0.2 mm. broad at base, weakly glochidiate, not at all to slightly confluent at base.

DISTRIBUTION OF SPECIES: West Pakistan, Kashmir, Tibet (?).

3a. Var. **spathulatum.**

Nutlets 2–2.5 mm. long, 1.3–1.5 mm. broad, minutely hairy on both surfaces, appendages usually not confluent at base.

West Pakistan: GILGIT AGENCY: Baltistan, Lamchau Nala, above Dras, 3700–4000 m., *Duthie 13786, 13767* (K).

Kashmir: Poonch, near Bedori, rocks, 3300 m., *Rashid, Nasir & Stewart 23942* (BM), *R. R. Stewart & Nasir 24038* (BM), *23924* (K); LADAK: Tog, on rocky slopes, 5000 m., *Koelz 2641* (GH); Ke La, 6000 m., in wet gravel, *Koelz 2508* (GH, K, US). Miscellaneous: Tibet Occ., Herb. Ind. Or. Hook. f. & Thoms. *Thomson 11* (GH).

3b. Var. **thomsonii** (C. B. Clarke) Kazmi, comb. nov.

Omphalodes thomsoni C. B. Clarke in Hook. f. Fl. Brit. India **4**: 155. 1883.
Eritrichium thomsoni (C. B. Clarke) I. M. Johnston, Jour. Arnold Arb. **21**: 53. 1940, non *E. strictum* var. *thomsoni* C. B. Clarke *l. c.* 164.

TYPE: Western Tibet: Nubra, 13,000 ft., *Thomson 8* (K).

Nutlets 3–3.5 mm. long, 2–2.5 mm. broad, usually glabrous, appendages more or less confluent at their bases.

Kashmir: LADAK: Tsullak, by side of rocks on dry banks along streams, 5300 m., *Koelz 2479* (GH); Rupshu, Tso Morari Korzok, on sandy slopes from side of rocks, 5000 m., *Koelz 2198* (GH, US); Korzok, 5000 m., *Koelz 2206a* (GH, US).

Eritrichium spathulatum may be distinguished from the closely related *E. fruticulosum* by its broader, ovate, sessile cauline leaves, covered with unequal trichomes and its larger nutlets; and from *E. canum* by its more herbaceous, decumbent habit, its broader cauline leaves, and the much shorter appendages on the margins of the nutlets.

4. **E. patens** Decne. in Jacquem. Voy. Inde Bot. 125. 1844; DC. Prodr. **10**: 128. 1846.

TYPE: D'Regui ad Tchini, Jul. 14. 1830, *Jacquemont 1316* (P-holotype, GH-isotype).

Erect perennial herb to 35 cm. tall. Stems woody at the base, many simple or branched above, brownish, densely covered with white, stiff, subappressed trichomes. Basal leaves petiolate, petioles up to 20 mm. long, slender, hairy; lamina linear, up to 20 mm. long, 1–1.5 mm. broad, entire, acutish, covered densely on both surfaces with short, stiff, appressed white trichomes, sometimes arising from tiny white tubercles, nerves inconspicuous; cauline leaves similar to the basal leaves, sessile, up to

15(–20) mm. long, 1–1.5 mm. broad, sometimes with comparatively longer trichomes below and at the margins. Inflorescence terminal or sometimes axillary, simple to germinate, bracteate, many flowered; pedicels up to 6 mm. long, slender, pubescent, recurved in fruit. Calyx divided nearly to the base, lobes lanceolate, pubescent, acute, 1–1.5 mm. long, 0.2–0.3 mm. broad, slightly enlarged in fruit. Corolla blue, campanulate, tube equalling the calyx, lobes 2 mm. long, 1.5 mm. broad, ovate, patent. Nutlets 4, excluding appendages 1.5 mm. long, 1 mm. broad, roundish at the base, acutish above, outer surface convex or slightly raised longitudinally in the middle, usually tuberculate, sometimes minutely hairy, trichomes arising from minute tuberculate bases, inner surface glabrous, margined with distant, glochidiate appendages, 0.2 mm. long, 0.1 mm. broad at base and not confluent.

DISTRIBUTION: West Pakistan, Kashmir, northwest India, Tibet.

West Pakistan: GILGIT AGENCY: Baltistan, Hushe to Brumi on the way from Hushe up to the Sospor glacier, *Schlagintweit 6006* (BM).

Kashmir: Hab. Tibet Occ., 13,000–14,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (BM); without locality, 1835, *Royle* (K, mounted with Clarke's *No. 30370c* of Aug. 10, 1876).

Brand (Pflanzenr. IV. **252**(Heft 97): 199. 1931) has placed *E. patens* in the synonymy of *Lappula barbata* var. *cariensis* but examination of the type showed it is an *Eritrichium*. *Eritrichium patens* closely resembles *E. fruticulosum*, from which it differs in its stout, densely pubescent, erect stems, very narrow, pubescent, basal leaves, and distinctly sessile cauline leaves. The nutlets of *E. patens* are comparatively smaller than those of *E. fruticulosum*. They are tuberculate on the outer face and glabrous on the inner side, while those of *E. fruticulosum* are not tuberculate but are pubescent all around. *Eritrichium patens* also has much shorter appendages at the margins of nutlets compared to *E. fruticulosum*.

5. **E. canum** (Benth. in Royle) Kitamura, Act. Phytotax. Geobot. **19**: 103. 1963; Fl. Pl. West Pakistan 121. 1964; Riedl in Rechinger, Fl. Iranica **48**: 64. 1967.

Echinospermum canum Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 306. 1836.

Eritrichium strictum Decne. in Jacquem. Voy. Inde Bot. 125. 1844; DC. Prodr. **10**: 128. 1846; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 164. 1883.

Eritrichium strictum var. *thomsoni* C. B. Clarke *l. c.*

Eritrichium longifolium Decne. in Jacquem. *l. c.* 124. *t. 129*. DC. Prodr. **10**: 125. 1846.

Myosotis longifolia Decne. in Jacquem. *l. c.*

Eritrichium rupestre (Pall.) Bunge α *genuinum* Herder, Acta Horti Petrop. **1**: 539. 1872.

Eritrichium rupestre (Pall.) Bunge var. *pectinatum* (Pall.) Brand, Pflanzenr. IV. **252**(Heft 97): 191. 1931, *pro parte* non *E. pectinatum* (Pall.) DC. Prodr. **10**: 128. 1846.

Eritrichium sericeum Aitch. Jour. Linn. Soc. Bot. **19**: 178. 1882, *non* DC. *l. c.*

TYPE: Lippa and Pangee in Kunawur, Kherang Pass, *R. Inglis s.n.* (K).

ICON.: Jacquem. Voy. Inde Bot. *t. 126.* 1844.

Perennial, usually erect, sometimes decumbent, up to 40 cm. tall. Stems woody at base, thick, grayish or white, simple or branched in the upper part, densely covered with appressed white trichomes. Basal leaves petiolate, petioles up to 50 mm. long, hairy, more or less broad at the base; lamina narrowly lanceolate, acutish, gradually attenuated towards the petioles, to 80 mm. long and 6 mm. broad, covered densely on both surfaces with short, white, appressed trichomes; middle cauline leaves many, sessile, lanceolate, up to 30 mm. long and 5 mm. broad, obtuse or sometimes roundish at apex, gradually becoming reduced in size above; upper cauline leaves ovate, acute. Inflorescence simple, geminate or ternate, up to 15 cm. long, many flowered, bracteate, bracts linear, those of the upper flowers very short, pedicels in flower short, in fruit up to 10 mm. long, erect, usually straight, pubescent. Calyx divided nearly to the base, lobes ovate, 1 mm. long, 0.6 mm. broad, in fruit enlarged to nearly twice their size, densely pubescent, obtuse or sometimes roundish at apex. Corolla bright blue with a yellow or orange eye, rotate-campanulate, tube slightly shorter than the calyx, lobes ± 3 mm. long and broad. Nutlets 4, (excluding appendages) 2 mm. long, 1.5 mm. broad, outer face plane or slightly concave, covered loosely to densely with thin short trichomes, rarely glabrous, inner side glabrous to pubescent or sometimes slightly tuberculate, margins appendiculate, appendages irregular, up to 1 mm. long, confluent at base, glochidiate at apex.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir, northwest India, and S.W. Tibet.

West Pakistan: CHITRAL STATE: Haute vallée de Yarkhun, Hautes Páturages, 4000 m., *Schmid 2283* (BM); upper Yarkhun valley, Pamir, *Schmid 30* (BM). GILGIT AGENCY: Chhantir gah, *Schmid 2163* (K). HAZARA DIST.: Kaghan valley, between Batakundi and Burawai, *Burtt & Reshan Din 922* (E). KURRAM AGENCY: Kurram valley, Kaiwas, Mt. Sikaran, 3300 m., *Aitchison s.n.* (GH); Kurram valley, *Harsukh 15408* (K); Safed Keh, north of Kurram valley, *Collett 110, 84* (K) Shalozan, ca. 2700 m., *Kazmi 204b* (PES); Ziran, *Kazmi s.n.* (PES). SWAT STATE: Batam above Ushu. 3000 m., *Rehman* in *R. R. Stewart 25366* (BM, MICH). Miscellaneous: N. W. F. P. (det. *Jafri*) *s.n.* (E). Reported from Baluchistan, *Lace.*

Kashmir: Sonamarg, *C. B. Clarke 30873* (K), *30873H* (BM, type of *E. strictum* var. *thomsoni*), 3000 m., *Rich 1119* (K), *R. R. Stewart 6403, 6751* (K), *9291, 12422a* (GH); Gagangu to Sonamarg, *Young s.n.* (BM); vicinity of Sonamarg, on Sind river, 50 road-miles east-northeast of Srinagar, *Dickason 102* (MICH); vicinity of Pahlgam on east of Lidder river, 27 road-miles north of Islamabad, *Dickason 103, 104* (MICH); vicinity of Baltal, on Sind river, 59 road-miles east-northeast of Srinagar, 3100 m., *Dickason 105* (MICH); Pangtaran to Thanin, *Young s.n.* (BM); Pir Panjal, 3300 m., *Drummond 14019* (E); upper Sheshnag valley, 3700 m., *Drummond 14186* (E); near Aliabad, 2800 m., *Drummond 13924* (E); above Kainmal, Lidder valley, 3500–4000 m., *Duthie 13138* (E);

Sind valley, Baltal, 3100 m., 30. 7. 1891, *Gammie s.n.* (K), *Duthie 11556* (E); Gumber valley, Sind valley, 3800 m., *Ludlow & Sherriff 7643* (BM); Zojibal Gali, 4300 m., *Polunin 56/744* (BM); Zojibal, 4000 m., in rocks and pathsides, bright blue flowers, *Pinfold 309* (BM); Zoji Pass, 3500 m., *R. R. Stewart 21199* (US); Upper Lidder valley, to Nar Nag, 2800 m., *R. R. Stewart 12949* (GH); Barpu Glacier, left bank, 4100 m., *Russell 1110* (BM); between Turmun and Mekerum, 3600–4000 m., *Russell 1230, 1219* (BM); Hispar Glacier, Chokutens, 3700 m., *Russell 1204* (BM); Zaskar, Lagong, 4500 m., *Koelz 5417* (GH, MICH, US); Kargia, 4500 m., *Koelz 5512* (GH, MICH, US); Chumikmarpe, Kargia, 4500 m., *Koelz 5355* (GH, MICH, US); Kangi La to Rungdum, 4000 m., *Koelz s.n.* (GH); Tsultak, 5000 m., *Koelz 2479a* (GH); Kamri Bungalow, 3300 m., *R. R. Stewart 22718* (GH); Kishtwar, Bubang on Suru Pass via Pashmin down to Nobug, *Schlagintweit 10145* (GH); Ladak, Khardong Pass, *Meinertzhagan 43* (BM), 5000–5600 m., *Miss C. C. Burt 153* (E); Khardong La, Leh, 5000 m., *Ludlow & Sherriff 8427* (BM); Hanu Yogma via Handamir up the Chorbat La Pass, *Schlagintweit 6508* (US); Tog, 3300 m., *Koelz 2611* (US); Skyangpoche, Karakorum trade route, 5100 m., *Ludlow 558* (BM); Hanupalta, 4500 m., *Osmaston 38* (K); Leh, across the pass north of Leh to Digger, left side of Shayok river, *Schlagintweit 6322* (GH). Miscellaneous: Hab. Tibet Occ., 13,000–14,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH); Herb. East India Co. *Falconer s.n.* (GH).

The most common species of *Eritrichium* in the northern parts of our area, *E. nanum* is very variable in its habit, ranging from tall and erect to low and decumbent. The shape of the leaves varies from linear to linear-lanceolate, or sometimes even to oblong, with obtuse or roundish apices. Similarly the stems, leaves, and branches are found covered with different densities of silvery-white to grayish-white trichomes. Its closest relatives are *E. patens* and *E. fruticulosum*. *Eritrichium nanum* differs from *E. patens* in larger, ovate nutlets, which are (excluding marginal appendages) 2 mm. long and 1.5 mm. broad, and their longer marginal appendages, up to 1 mm. long, always longer than 0.2 mm., and confluent at their bases. It is very easily distinguished from *E. fruticulosum* by its larger, sessile and much more densely pubescent leaves as well as by the characters of its nutlets noted above.

11. **Lasiocaryum** I. M. Johnston, Contr. Gray Herb. **75**: 45. 1925.

Oreogenia I. M. Johnston, Contr. Gray Herb. **73**: 65. 1924.

TYPE SPECIES: *Lasiocaryum munroi* (C. B. Clarke) I. M. Johnston.

Annual or perennial low villous herbs. Leaves alternate. Inflorescence bracteate. Calyx divided to the base, 5-lobed. Corolla blue, transversely plicate internally below the middle, tube cylindrical, more or less equalling the calyx, lobes imbricate, orbicular, obtuse; faucal appendages distinct. Stamens 5, inserted on the corolla tube, included; anthers ovate, slightly obtuse. Ovary 4-lobed, style short, stigma capitate. Nutlets 4, erect, emarginate, keeled longitudinally on the inner face, attached nearly

along their whole length to the columnar gynobase, dorsally strigose, hispidulous, convex, carinate in the middle.

Species 4 to 5 distributed from Iran to Central China.

Ivan M. Johnston (*l. c.* 1924) described this genus, based on *Eritrichium munroi* C. B. Clarke, and named it *Oreogenia*. Later (*l. c.* 1925) realizing that the name *Oreogenia* has a practical if not an exact homonym in Watson's *Orogenia* (Bot. King Exped. 120. 1871) and since the two names are etymologically the same in origin and differ only in the presence or absence of a connecting vowel, he substituted a new name *Lasiocaryum* (*l. c.* 1925) for the genus. Brand (Pflanzenr. IV. **252**(Heft 97): 185. 1931) and Riedl (in Rechinger, Fl. Iranica **48**: 66. 1967) have given priority to *Oreogenia*, but I agree with Johnston and maintain his substituted name *Lasiocaryum*.

Key to the Species

a. Calyx lobes broadly lanceolate to oblong-ovate, 1.5–2 mm. long; corolla 2.5 mm. long, corolla lobes 0.5 mm. long and broad. ..... 1. *L. munroi.*
a. Calyx lobes linear to linear-lanceolate 2–2.5 mm. long; corolla 2–3 mm. long, corolla lobes 1 mm. long and broad. ..... 2. *L. densiflora.*

1. **L. munroi** (C. B. Clarke) I. M. Johnston, Contr. Gray Herb. **75**: 46. 1925.

Eritrichium munroi C. B. Clarke in Hook. f. Fl. Brit. India **4**: 165. 1883; W. W. Smith, Rec. Bot. Serv. India **4**: 225. 1911.
Oreogenia munroi (C. B. Clarke) I. M. Johnston, Contr. Gray Herb. **73**: 66. 1924; Brand, Pflanzenr. IV. **252** (Heft 97): 185. 1931.

Type: Sikkim, Lachen (*Eritrichium* sp. no. 13, Herb. Ind. Orient. Hook. f. & Thoms.), *J. D. Hooker* (K-holotype, GH-isotype).

Annual 1–10 cm. tall. Stems many, slender, simple or branched, brownish, covered thinly or densely with thin, spreading trichomes up to 1 mm. long. Basal leaves in rosettes, obovate to spathulate, obtuse, margins entire, gradually attenuated towards the short petioles, nerves inconspicuous, to 11 mm. long and 3 mm. broad, covered on both surfaces by scattered, white, crisped, spreading trichomes up to 1 mm. long; cauline leaves gradually reduced in size towards the top. Inflorescence of dense terminal racemes, bracteate, bracts leaflike. Pedicels pubescent, erect, short in flower, in fruit up to 5 mm. long. Calyx divided to the base, lobes lanceolate to oblong-ovate, pubescent, erect, 1.5–2 mm. long, 0.3 mm. broad. Corolla sky blue with white eye, tubular, 2.5 mm. long, tube equalling the calyx, lobes 0.5 mm. long and broad, roundish; faucal appendages distinct. Nutlets 4, brownish, oblong-ovoid, 1 mm. long, 0.5 mm. broad, minutely transversely wrinkled and slightly hirtellous. Stigma capitate, slightly exceeding the nutlets.

DISTRIBUTION: Western Himalayas, from Kashmir to Sikkim in alpine zone.

Kashmir: LADAK: Ke La, 6000 m., *Koelz 2508r* (GH, MICH); Nanu, *Koelz 2538a* (MICH); Tsakzhun Tso, *Koelz 2402* (MICH). RUPSHU: Puga, *Koelz 2183* (MICH).

2. **L. densiflorum** (Duthie) I. M. Johnston, Jour. Arnold Arb. **21**: 51. 1940.

Eritrichium densiflorum Duthie, Kew Bull. **1912**: 39. 1912.
Oreogenia Duthieana Brand, Repert. Sp. Nov. **22**: 103. 1925; Pflanzenr. IV. **252**(Heft 97): 186. 1931.
Microcaryum Duthieanum Brand, Repert. Sp. Nov. **22**: 101. 1925; Pflanzenr. IV. **252**(Heft 97): 202. 1931.

TYPE: Phembu La, 10–15 miles north of Lhasa, Sept. 1904, *H. J. Walton 1547* (K-lectotype), *s.n.* (A).

Perennial 4–10 cm. tall. Stems many, rigid, usually branched; branches spreading, stem and branches covered with long, thin, subappressed or spreading trichomes. Basal leaves obovate to spathulate, margins entire, apices obtuse or roundish, gradually attenuated towards short petioles up to 15 mm. long, 5 mm. broad, covered on both surfaces loosely with thin, white, crisped, trichomes up to 2 mm. long, which arise from prominent white tuberculate bases; cauline leaves sometimes larger than the basal leaves, sessile to subamplexicaul, obtuse; upper cauline leaves ovate, much shorter than middle cauline leaves. Inflorescence terminal, racemes compact, flowers many, subsessile to short pedicellate, pedicels up to 3 mm. long in fruit, pubescent, erect; bracts foliaceous. Calyx divided to the base, lobes erect, linear to linear-lanceolate, acute, 2–2.5 mm. long, ca. 0.2 mm. broad, more pubescent on the margins. Corolla pale blue with yellow eye, tubular-campanulate, 2.5–3 mm. long, tube usually slightly exceeding or sometimes equalling the calyx, lobes 1 mm. long and broad, roundish, spreading; faucal appendages well developed. Nutlets 4, similar to those of *L. munroi*.

DISTRIBUTION: Western Himalayas from Kashmir to Bhutan.

Kashmir: LADAK: Gya, *Koelz 6437* (MICH).

Lasiocaryum densiflorum is closely related to *L. munroi*, but it is coarser and more spreading. It has larger flowers with narrower sepals compared to those of *L. munroi*.

The binomial *Microcaryum duthieanum* Brand (*l. c.*) is essentially a name for *L. densiflorum*. Brand seems to have discarded Duthie's trivial name since he believed Duthie's species was an aggregate. Duthie's description, however, applies well to the readily recognizable *L. densiflorum*. Duthie did not indicate the type for his *Eritrichium densiflorum* and has cited a number of collections. The sheet of H. J. Walton bears the name

of the new species "*E. densiflorum*" in Duthie's handwriting and may be taken as the lectotype of the species.

12. **Hackelia** Opiz in Berchtold Oek.-techn. Fl. Bohmens 2(2): 147. 1839.

TYPE SPECIES: *H. deflexa* (Wahlenb.) Opiz.

Usually perennial or biennial, rarely annual herbs. Leaves alternate. Inflorescence terminal or axillary, often paniculate, naked or rarely bracteate. Pedicels recurved or deflexed in fruit. Calyx divided to the base or rarely up to two-thirds its length. Corolla cylindrical, infundibuliform, campanulate or subrotate; faucal appendages usually large, variable. Stamens included. Style and stigma simple. Gynobase pyramidal, shorter than broad. Nutlets surpassing the style, attached by a large oblique, submedial, ovate or deltoid areola; ventral keel extending only over the upper half of the nutlet.

Species 40 to 45, most occurring in western North America, with 7 to 8 species in the cooler parts of Europe and Asia.

KEY TO THE SPECIES

a. Cauline leaves linear, up to 1 mm. broad. ..... 2. *H. thymifolia.*
a. Cauline leaves lanceolate to ovate, more than 4 mm. broad.
  b. Leaves more or less lustrous on the upper surface, glabrous or nearly so; corolla white or white with blue or purple spots between the bases of the lobes; nutlets bearing appendages on the margins as well as on the dorsal surface. ..... 4. *H. macrophylla.*
  b. Leaves with abundant minute trichomes on the upper surface, not lustrous; corolla pale to dark blue; nutlets bearing appendages only on the margins, dorsal surface smooth to minutely setose.
    c. Marginal appendages shorter than the body of the nutlet.
      d. Nutlets ca. 5 mm. long. ..... 1. *H. deflexa.*
      d. Nutlets ca. 2 mm. long. ..... 3. *H. meeboldii.*
    c. Marginal appendages subequal to longer than the body of the nutlet.
      e. Style elongate, 2–2.5 mm. long; corolla 10–14 mm. in diameter, pale blue; faucal appendages longer than broad 1–1.3 mm. long, 0.8 mm. broad; cauline leaves broadly lanceolate, 6–18 cm. long, 2–8 cm. broad, lowest ones not cordate. ..... 6. *H. stewartii.*
      e. Style short, 0.2–0.8 mm. long; corolla usually less than 10 mm. in diameter; faucal appendages broader than long, 0.3–0.8 mm. long, 0.6–0.9 mm. broad; cauline leaves ovate, 6–9 cm. long, 2.5–5 cm. broad, lowest ones usually cordate. ..... 5. *H. uncinata.*

1. **H. deflexa** (Wahlenb.) Opiz in Berchtold, Oek.-techn. Fl. Bohmens 2(2): 147. 1839; I. M. Johnston, Contr. Gray Herb **68**: 45. 1923; Brand, Pflanzenr. IV. **252**(Heft 97): 123. 1931, excl. var. *pumila*; M. Pop. Fl. URSS **19**: 480. 1953.

Myosotis deflexa Wahlenb. in Sv. Vet-akad. Handl. **31**: 113. 1810.

Echinospermum deflexum Lehm. Asperif. **2:** 120. 1818; DC. Prodr. **10:** 135. 1846; Ledeb. Fl. Rossica **3:** 154. 1847.
Rochelia deflexa Roem. & Schult. Syst. **4:** 109. 1819.

TYPE: In umbrosis petrosis ad radices Alpinum Nordlandiae Norvegiae, Lapponiae Lulensis, *Wahlenberg s.n.* (UPS).

ICON.: Wahlenb. l. c. *fig. 4.* 1810, under *Myosotis deflexa*; Oeder, Fl. Dan. 9: *t. 1568.* 1816, under *Myosotis deflexa*; Brand, l. c. *fig. 14 A–B.*

Biennial (?), erect herb, 15–55 cm. tall. Stems usually simple, rarely branched, covered on the lower part with spreading and on the upper part with appressed white trichomes. Lower cauline leaves petiolate, usually oblong-lanceolate, rarely ovate, (including petioles) 10–15 cm. long, 10–20(–30) mm. broad, upper cauline leaves sessile, oblong-lanceolate to linear-lanceolate, narrowed towards the base, 4–8 cm. long, 5–12(–20) mm. broad; all the leaves covered on both surfaces with white, spreading trichomes. Inflorescence terminal or subterminal, lax, bracteate. Pedicels in fruit longer than calyx, reflexed. Calyx divided nearly to the base, lobes ovate, hairy, ca. 2 mm. long. Corolla blue, subrotate, nearly twice the length of the calyx; faucal appendages large, subtrapeziform, papillose. Nutlets ca. 5 mm. long, ovoid, granulate, appendiculate at the margins, appendages uniseriate, slightly confluent at base, glochidiate at apex, dorsal surface of the nutlet plane, carinate, ventral surface convex.

DISTRIBUTION: Europe, Asia, and North America.

Kashmir: LADAK: Skirbichan, *Meebold 4204* (Breslau; Pangi, *Stolezka s.n.* (K).

2. **H. thymifolia** (DC.) I. M. Johnston, Jour. Arnold Arb. **21:** 54. 1940.

Echinospermum thymifolium DC. Prodr. **10:** 136. 1846.
E. deflexus var. *pumilum* Ledeb. Fl. Ross. **3:** 155. 1847.
Lappula thymifolia Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. **3a:** 107. 1897.
Hackelia deflexa var. *pumila* (Ledeb.) Brand, Pflanzenr. IV. **252**(Heft 97): 126. 1931.
Hackelia thymifolia (DC.) M. Pop. Fl. URSS **19:** 480. 1953, *syn. nov.*

TYPE: In Mongolia sinensi et ad Selenginsk Mongoliae, *Turcz. s.n.* (G–DC).

Annual, erect, 10–30 cm. tall. Stems branched above, covered with appressed, white trichomes. Basal leaves short petiolate, (including petioles) 10–25 mm. long, 2–5 mm. broad; cauline leaves linear, 3–5 mm. long, 1 mm. broad, covered on both surfaces with short, spreading, white trichomes, arising from tuberculate bases. Inflorescence long, bracteate, bracts leaflike, lateral or opposite the pedicels. Pedicels in fruit shorter, or at the maximum, equalling the calyx, deflexed. Calyx and corolla more or less like those of *H. deflexa,* smaller in size. Nutlets 2 mm. long,

heteromorphic, one nutlet muricate, the other three broadly margined and smooth.

DISTRIBUTION: Kashmir, Central Asia.

Kashmir: RUPSHU: Kiangchu, *Koelz 6619* (MICH).

Very closely related to *Hackelia deflexa*, *H. thymifolia* is differentiated from that species by having much smaller, more slender, and much branched stems; smaller corollas and fruits; and proportionately much shorter pedicels.

3. **H. meeboldii** Brand, Repert. Sp. Nov. **22**: 104. 1925; Pflanzenr. IV. 252(Heft 97): 135. 1931.

TYPE: Ladak: Kangi La, beide Seiten, ca. 4000 m., *Meebold 4205* (Breslau).

Perennial, shrubby, erect, 12–50 cm. tall. Stem profusely leafy, densely strigose. Lower cauline leaves petiolate, (including long petioles) 50–60 mm. long, 4–5 mm. broad, linear-lanceolate, short cuspidate at apex, gradually narrowed into the petiole at base. Inflorescence basal, axillary to terminal, lax, elongate, bracteate. Pedicels in flower short, in fruit much elongated, longer than the calyx. Calyx divided nearly to the base, lobes in flower linear, ca. 2 mm. long, spreading and not much elongated in fruit. Corolla blue, rotate, limbs divided to the base, 9 mm. in diameter; faucal appendages semilunar, emarginate. Nutlets brownish, ovoid, ca. 2 mm. long, inconspicuously and minutely setose on all the sides, dorsal face concave, short aculeate at the margins, carinate ventrally from the top to the middle.

DISTRIBUTION: Kashmir.

Kashmir: Between Ladak and Zanskar, both sides of Kangi La, 4000 m., *Meebold 4205* (Breslau-type).

I did not see any specimen of the above species and the description has been given according to Brand (*l. c.*). Very little material of all the above three species has been collected from our area and a thorough study with more material is needed.

4. **H. macrophylla** (Brand) I. M. Johnston, Contr. Gray Herb. **68**: 45. 1923; Brand, Pflanzenr. IV. 252(Heft 97): 120. 1931.

Cynoglossum uncinatum var. *laxiflorum* Royle ex Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1836.

Cynoglossum macrophyllum Royle ex Benth. in Royle, *l. c.* 1836; DC. Prodr. **10**: 136. 1846, *nomen nudum*.

Echinospermum glochidiatum var. *laxiflorum* (Royle ex Benth.) DC. Prodr. **10**: 136. 1846.

Lappula macrophylla Brand, Repert. Sp. Nov. **14**: 146. 1915.

TYPE: Nagkanga, Tuan et Urrukta, *Royle s.n.* (K).

ICON.: Brand, l. c. *fig. 13. A–C.* 1931.

Perennial, erect herb to 80 cm. tall. Stems in the upper part glabrous, loosely pubescent below. Cauline leaves petiolate, ovate to suborbicular, (including petioles) 10–20 cm. long, 5–13 cm. broad, glabrous and lustrous on the upper surface, on the lower surface with minute scattered trichomes. Pedicels in fruit usually longer than the calyx. Calyx divided to the base, lobes broadly lanceolate, acute, in flower 3–4 mm. long, not much enlarged in fruit. Corolla white with blue or purple spots between the bases of the lobes. Nutlets 6.5 mm. long, hardly winged, bearing appendages on the dorsal surface as well as on the margins, appendages glochidiate at apex sometimes up to 13 mm. long. Style about 1/3 the length of calyx.

DISTRIBUTION: West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Mirga, *Gatacre 17353* (DD, K); Ziarat, *Toppin 431* (K); HAZARA DIST.: Kaghan Valley, between Shogran and Sari Rest House, ca. 3000 m., *Kazmi 2126b* (PES); Shogran, 2000 m., *Nasir 3923* (RAW); Nathiagali, Mokshpuri, 3000 m., *Kazmi 798b* (PES); Changla Forests, *Miss Sanders s.n.* (K). SWAT STATE: Bishgram, *R. R. Stewart s.n.* (RAW); Utror, *Kazmi 199b* (PES); Bahrain, *Kazmi 220b* (PES).

Kashmir: Pangi, *Watt s.n.* (K); Aru, 2700 m., *Drummond 14116* (K); Badwan, 2500 m., *Coventry 1488* (K). Reported from: Gulmarg, 3000 m., *Gammie s.n.*; Noburg, 2400 m., *Meebold 4239.*

5. **H. uncinata** (Benth.) C. E. C. Fischer, Kew Bull. **1932**: 298. 1932.

Cynoglossum uncinatum Benth. in Royle, Illustr. Bot. Himal. Mount. **1**: 305. 1836.
C. Roylei Wall. in G. Don, Gen. Syst. **4**: 356. 1838.
C. laxum G. Don, *Ibid.*
Rindera glochidiata Wall. Cat. no. 926. 1828, *nomen nudum.*
Echinospermum glochidiatum DC. Prodr. **10**: 136. 1846.
Paracaryum glochidiatum Benth. & Hook. f. Gen. Pl. **2**: 850. 1876; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 161. 1883.
Lappula glochidiata Brand, Repert. Sp. Nov. **16**: 146. 1915.
Hackelia Roylei (Wall.) I. M. Johnston, Contr. Gray Herb. **68**: 45. 1923.
H. glochidiata (Wall.) Brand, Pflanzenr. IV. **252**(Heft 97): 119. 1931.

TYPE: Choor, Acharanda, Dokree, Kunawur, *Royle s.n.* (K).

Erect, perennial herb, 60–80 cm. tall. Stems fistulous, branched, sparsely setulose. Basal leaves petiolate, petioles 25–30 cm. long, lamina, obovate, 8–9 cm. long, 4–5 cm. broad; cauline leaves short petiolate, ovate to elliptic, (including petioles) 6–12 cm. long, 2–5 cm. broad, 5–7-nerved, acuminate, rounded at the base, truncate or subcordate, minutely hairy on both surfaces. Inflorescence terminal to subterminal, bifurcate, elongate. Pedicels in fruit not longer than the calyx. Calyx divided to the base, lobes ovate, pubescent, obtuse. Corolla blue, campanulate-rotate,

tube equalling the calyx, limbs divided to the base, lobes broadly ovate, ca. 7 mm. long; faucal appendages subquadrate. Stamens attached to the middle of corolla tube, anthers not exceeding the faucal scales, filaments short. Nutlets ovoid, narrowed towards the apex, broadly winged, excluding the wings 4–5 mm. long, wings densely appendiculate, appendages glochidiate at apex, long. Style about half the length of calyx.

DISTRIBUTION: West Pakistan, Kashmir, northern India to Sikkim.

West Pakistan: HAZARA DIST.: Kaghan Valley, Shogran, 2700 m., *Kazmi 2171b* (PES); Kamalbun Forests, *Kazmi 79b* (PES); Gallies, Nathiagali to Ghoragali, ca. 5000 m., *Kazmi 327b* (PES); Nathia Gali, near Government House, *Kazmi 793a* (PES); Miranjani, *R. R. Stewart 28698, 28866* (RAW); Siran Valley, below Shaheed Pani, about 6 miles above Dadder, *Kazmi s.n.* (PES). RAWALPINDI DIST.: Murree Hills, between Jhikagali and Murree, on Kohala road, *Kazmi s.n.* (PES). SWAT STATE: Utror, Bishgram, *R. R. Stewart s.n.* (RAW); near Madian, *Kazmi s.n.* (PES).

Kashmir: Poonch, between Alibad and Kuthnar, *R. R. Stewart s.n.* (RAW). Reported from: Liddar Valley, near Sonsanala, 4500 m., *Duthie 13369*.

6. **H. stewartii** I. M. Johnston, Jour. Arnold Arb. 37: 303. 1956.

TYPE: Kashmir: Rajdhian Pass, *R. R. Stewart 19526* (GH-holotype).

Perennial, erect, 60–100 cm. tall. Stems fistulous, to 8 mm. thick at the base, branched in the upper part, branches at flowering time 5–20 cm. long, pubescent. Cauline leaves petiolate, petiole 5–35 mm. long, lamina lanceolate, 6–18 cm. long, 2–8 cm. broad, acuminate, gradually narrowed towards the base, on the upper surface covered loosely with patent trichomes to 0.5 mm. long, arising from minute tuberculate bases, on the lower surface densely covered with soft, white, subappressed trichomes not arising from tuberculate bases, these denser on the nerves. Inflorescence solitary or geminate, terminal, 7–15 cm. long, ebracteate or bearing a single leaflike bract, 1–4 mm. long. Pedicels in flower up to 3 mm. long, in fruit elongated to 5 mm., reflexed, hairy. Calyx divided nearly to the base, lobes densely hairy, in flower 1.5–2.5 mm. long, 0.6–1 mm. broad, in fruit more or less ovate-lanceolate to 3.5 mm. long and 2 mm. broad. Corolla blue, 10–14 mm. in diameter, tube 1.5–2 mm. long, lobes rounded, patent, 4 mm. in diameter; faucal appendages oblong, 1–1.3 mm. long, 0.8–1 mm. broad, villous at the margins. Nutlets 4.5–5 mm. long, 2–3 mm. broad, winged at the margins, wings often 0.2–2 mm. broad, appendiculate, appendages uniseriate, subulate, 1–3 mm. long, glochidiate at their apices; dorsal middle area not at all to rarely inconspicuously hispidulous. Gynobase 2.5–3 mm. long, ca. 2 mm. broad at the base. Style elongate, 2–2.5 mm. long, often exserted.

DISTRIBUTION: Kashmir.

Kashmir: Rajdhian Pass, July 19, 1940, *R. R. Stewart 19526* (GH-holotype); trip to Gurais, *R. R. Stewart 12955* (G); Sonamarg, 3500 m., *R. R. Stewart 12959* (G); Killanmarg, 3000 m., *R. R. Stewart 8604A* (G); Pahlgam, 3000 m.,

R. R. Stewart 12956 (G); mountains opposite Pahlgam, 3300 m., *R. R. Stewart 21816* (G); Zur Nar Arie, Liddar Valley, *R. R. Stewart 21563* (G); 6 miles south of Karagbal, fir forest, 2700 m., *Koelz 9239* (G).

Hackelia stewartii is closely related to *H. uncinata* and *H. macrophylla*, and in gross habit is intermediate between them. It is readily recognizable from *H. uncinata* by having the cauline leaves broadly lanceolate, acuminate, and none of them cordate at base, by faucal appendages of the corolla longer than broad and the longer style; and from *H. macrophylla* by having pubescent leaves, blue corolla, and bearing appendages only on the margins of nutlets.

13. **Microula** Benth. in Benth. & Hook. f. Gen. Pl. 2: 853. 1876.

Tretocarya Maxim. Bull. Acad. Sci. St. Pétersb. **27**: 505. 1881; Mél. Biol. **11**: 270. 1881.

TYPE SPECIES: *M. tibetica* Benth.

Perennial; leaves in rosettes; flowers and fruits axillary. Calyx divided to the base, in fruit much enlarged and patent. Corolla broad cylindrical, lobes rounded, obtuse; faucal appendages semilunar. Stamens included; anthers ovate, filaments short. Gynobase pyramidal with 4 not very conspicuous swellings. Style longer than gynobase; stigma capitate. Nutlets 4 with a thick median dorsal crest.

Ivan M. Johnston (Contr. Gray Herb. 73: 62. 1924) recognized seven species which were later transferred to the other genera by Brand (Pflanzenr. IV. 252(Heft 97): 25. 1931), except for *M. tibetica*, a species distributed in the western Himalayas and western Tibet.

M. tibetica Benth. in Benth. & Hook. f. Gen. Pl. **2**: 853. 1876; Maxim. Bull. Acad. Sci. St. Pétersb. **26**: 501. 1880, Mél. Biol. **10**: 682. 1880; Hemsley in Hooker's Ic. Pl. **26**: *t. 2562*. 1898, Jour. Linn. Soc. Bot. **35**: 192. 1902; I. M. Johnston, Contr. Gray Herb. **73**: 62. 1924; Brand, Pflanzenr. IV. **252**(Heft 97): 25. 1931.

Tretocarya pratensis Maxim. Bull. Acad. Sci. St. Pétersb. **27**: 505. 1881; Mél. Biol. **11**: 272. 1881.

Microula tangutica Maxim. Bull. Acad. Sci. St. Pétersb. **26**: 500. 1880; Mél. Biol. **10**: 682. 1880.

Microula benthamii C. B. Clarke in Hook. f. Fl. Brit. India **4**: 167. 1883; Oliver in Hooker's Ic. Pl. **23**: *t. 2257*. 1893.

TYPE: not indicated.

ICON.: Hemsley, l. c. *t. 2562*. 1898; Oliver, l. c. *t. 2257*, under *M. benthamii*.

Perennial, acaulescent, with thick, unbranched root 5–15 cm. long. Leaves in rosettes, petiolate, petioles winged, flat, with longitudinal parallel veins, broad at the bases, pubescent; lamina ovate to oblong-ovate, usually 2 to 4 times as long as the petiole, margins usually entire, some-

R. R. Stewart 12956 (G); mountains opposite Pahlgam, 3300 m., *R. R. Stewart 21816* (G); Zur Nar Arie, Liddar Valley, *R. R. Stewart 21563* (G); 6 miles south of Karagbal, fir forest, 2700 m., *Koelz 9239* (G).

Hackelia stewartii is closely related to *H. uncinata* and *H. macrophylla*, and in gross habit is intermediate between them. It is readily recognizable from *H. uncinata* by having the cauline leaves broadly lanceolate, acuminate, and none of them cordate at base, by faucal appendages of the corolla longer than broad and the longer style; and from *H. macrophylla* by having pubescent leaves, blue corolla, and bearing appendages only on the margins of nutlets.

13. **Microula** Benth. in Benth. & Hook. f. Gen. Pl. 2: 853. 1876.

Tretocarya Maxim. Bull. Acad. Sci. St. Pétersb. 27: 505. 1881; Mél. Biol. 11: 270. 1881.

TYPE SPECIES: *M. tibetica* Benth.

Perennial; leaves in rosettes; flowers and fruits axillary. Calyx divided to the base, in fruit much enlarged and patent. Corolla broad cylindrical, lobes rounded, obtuse; faucal appendages semilunar. Stamens included; anthers ovate, filaments short. Gynobase pyramidal with 4 not very conspicuous swellings. Style longer than gynobase; stigma capitate. Nutlets 4 with a thick median dorsal crest.

Ivan M. Johnston (Contr. Gray Herb. 73: 62. 1924) recognized seven species which were later transferred to the other genera by Brand (Pflanzenr. IV. 252(Heft 97): 25. 1931), except for *M. tibetica*, a species distributed in the western Himalayas and western Tibet.

M. tibetica Benth. in Benth. & Hook. f. Gen. Pl. 2: 853. 1876; Maxim. Bull. Acad. Sci. St. Pétersb. 26: 501. 1880, Mél. Biol. 10: 682. 1880; Hemsley in Hooker's Ic. Pl. 26: *t. 2562*. 1898, Jour. Linn. Soc. Bot. 35: 192. 1902; I. M. Johnston, Contr. Gray Herb. 73: 62. 1924; Brand, Pflanzenr. IV. 252(Heft 97): 25. 1931.

Tretocarya pratensis Maxim. Bull. Acad. Sci. St. Pétersb. 27: 505. 1881; Mél. Biol. 11: 272. 1881.

Microula tangutica Maxim. Bull. Acad. Sci. St. Pétersb. 26: 500. 1880; Mél. Biol. 10: 682. 1880.

Microula benthamii C. B. Clarke in Hook. f. Fl. Brit. India 4: 167. 1883; Oliver in Hooker's Ic. Pl. 23: *t. 2257*. 1893.

TYPE: not indicated.

ICON.: Hemsley, l. c. *t. 2562*. 1898; Oliver, l. c. *t. 2257*, under *M. benthamii*.

Perennial, acaulescent, with thick, unbranched root 5–15 cm. long. Leaves in rosettes, petiolate, petioles winged, flat, with longitudinal parallel veins, broad at the bases, pubescent; lamina ovate to oblong-ovate, usually 2 to 4 times as long as the petiole, margins usually entire, some-

times irregularly dentate, round at apex, abruptly narrowed at base, upper surface covered densely and uniformly with trichomes 0.2–0.3 mm. long, intermixed with scattered, stout trichomes arising from large tuberculate bases and up to 1 mm. long, lower surface usually covered with long trichomes, rarely intermixed with short ones. Inflorescence interrupted, bracteate; flowers pedicellate, pedicels erect in flower, recurved in fruit. Calyx deeply divided, lobes ovate to broadly triangular, 1–1.5 mm. long ± 1 mm. broad at the base, enlarged in fruit, acute or sometimes obtusish at apex, pubescent. Corolla white to light blue, broadly cylindrical, tube usually equalling the calyx, glabrous, lobes ovate to rounded, 1–1.5 mm. long and broad, sometimes broader, veined, patent; faucal appendages 5, ovate to semilunar. Stamens included; anthers ovate, 0.6 mm. long, subsessile, inserted 0.7–1 mm. above the corolla base. Nutlets 4, white or bluish, ovate, acute at apex, round at base, tuberculate dorsally and at the margins, tubercles sometimes bearing tiny glochidiate appendages.

DISTRIBUTION: West Tibet, Kashmir, West Pakistan.

Kashmir: LADAK: Rupshu, Korzok, 5000 m., *Koelz 2209* (GH); Shushal, 4700 m., at the edge of lake, *Koelz 2443d* (GH); Taklung La, 5600 m., *Koelz 6495* (GH); Rupshu, Tso Kar, 4700 m., *Koelz 6609* (GH); Leh, Mashoe Nullah, 5300 m., *Ludlow & Sherriff 8455* (GH); Ladak, *Kohli 14* (K). Reported from: Karakorum: Tal des Indus, Chela & Lago Pancong, (Pampanini Fl. Carac. 179. 1930).

Bentham, in Genera Plantarum, has indicated no specimen as type. Probably this species is based on "West Tibet: Parang Pass, *T. Thomson* (K)."

14. **Trigonotis** Stev. Bull. Soc. Nat. Moscou **24**(1) : 603. 1851.

Eritrichium Sect. *Endogenia* & Sect. *Oreocharis* quoad species brevifloras A. DC. in DC. Prodr. **10:** 128. 1846.
Endogenia Lindl. Veg. Kingdom ed. 2. 256. 1847.
Zoelleria Warb. Bot. Jahrb. **14:** 123. 1892.
Havilandia Stapf, Trans. Linn. Soc. **4:** 209. 1894.
Pedinogyne Brand, Repert. Sp. Nov. **21:** 251. 1925.

TYPE SPECIES: *T. clavata* Stev.

Perennial, weak or diffuse, more or less pubescent, often caespitose herbs. Calyx 5-fid or 5-partite, strigose, in fruit not, or only slightly, enlarged. Corolla small, blue or white with 5 small, obtuse faucal appendages. Stamens 5, included, usually inserted at the middle of the corolla tube. Style short, stigma capitate. Nutlets 4, usually tetrahedral with 4 acute, rounded or winged marginate edges, hardly longer than broad; attachment scar of nutlets at the basal end of the ventral keel small, subsessile or stipitate, the stipe straight or abruptly bent on one side.

Species 35, distributed in Asia and temperate areas of Melanesia.

T. tibetica (C. B. Clarke) I. M. Johnston, Contr. Gray Herb. **75**: 48. 1925; Brand, Pflanzenr. IV. **252**(Heft 97): 200. 1931; Hao, Bot. Jahrb. **68**: 632. 1938; Banerjee, Bull. Bot. Surv. India **8**(3 & 4): 324. 1966.

Eritrichium tibeticum C. B. Clarke in Hook. f. Fl. Brit. India **4**: 168. 1883; Smith & Cav. in Rec. Bot. Surv. India **4**: 226. 1911; *Smith* l. c. **4**(7): 398. 1913.

Pedinogyne tibetica (C. B. Clarke) Brand, Repert. Sp. Nov. **21**: 251. 1925.

TYPE: Tibet; in Herb. Ind. Or. Hook. f. & T. Thoms., (as *Eritrichium* sp. nov. 17), *Thomson s. n.* (K-holotype, GH, CAL-isotypes).

ICON.: Banerjee, *l. c.* **8**(3 & 4): 324. *pl. 3. fig. a–f.* 1966.

Perennial, weak, diffuse. Stems many, 15–25 cm. long, covered with short appressed trichomes. Basal and lower cauline leaves petiolate, elliptic-ovate to lanceolate, to 20 mm. long and 8 mm. broad; upper cauline leaves subsessile, shorter and narrower, covered on both surfaces with short antrorsely appressed white trichomes. Inflorescence terminal, lax, helicoid at the top; pedicels erect or those of the lower fruits horizontal, 0.5–5 mm. long. Calyx divided to the base, lobes in fruit 1.5 mm. long, 1 mm. broad, ovate to broad-lanceolate, acutish, hairy, erect. Corolla white, campanulate, rimmed with sky-blue, with a yellow eye, 1 mm. long, lobes equalling the tube; faucal appendages semilunar. Stamens attached at the middle of the corolla tube, included. Nutlets 1 mm. long, tetrahedral, with 4 acute or submarginate edges, stipitate, stipe abruptly bent on one side, brown, glabrous, shining, attachment scar small, basal.

DISTRIBUTION: West Tibet, Kashmir, Nepal, Sikkim.

Kashmir: LADAK: Nanu, 4700 m., *Koelz 2349* (GH); Sakti, 4000 m., *Koelz 2502* (GH); between Chang La and Zingrul, 5500 m., *Koelz 2489b* (GH); Leh, in Herb. Ind. Or. Hook. f. & Thoms. *Thomson s.n.* (K). Reported from: Rupshu, Korzok, *Koelz 2209*; Zanskar, *Koelz A48*.

[*To be continued*]

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, VI. STAMENS AND YOUNG STEM*

WILLIAM C. DICKISON

THE DILLENIACEAE HAVE long been held to be a phylogenetically interesting though perplexing dicotyledonous family. This confusion has been the result, in part, of the fact that so little morphological-anatomical information was assembled concerning the group. The repeated descriptions of new features during the course of this series of investigations substantiates this fact. Thus there has previously been no foundation for making judgments on the taxonomic, phylogenetic, and distributional relationships of the family. I now feel, however, with the information presented in this paper, dealing with stamen morphology and young stem anatomy, that a sufficient amount of data has been gathered to warrant such a discussion.

All specimens studied have been cited with pertinent collecting data in previous papers in this series. Material was prepared according to the standard procedures for clearing and sectioning. Phloem was stained with lacmoid, a stain specific for callose, with excellent results.

STAMENS

Stamens of the subfamily Tetraceroideae (FIGURES 13, 14, 15, 16, 17) are all indefinite in number and characterized by a more or less broadened connective. Stamens are readily separated into filament, anther, and connective. The filament is filiform, free or occasionally basally fused in *Tetracera*. The largest number of stamens, from about fifty to over five-hundred, are found in *Tetracera*, although Hunter (1966) reports the outer stamens in New World species are frequently sterile. Raphides or crystal sand, are common in the connectives of stamens in all genera (FIGURE 18).

Each anther is comprised of 2 pairs of marginal, half-embedded microsporangia and a dilated connective. In *Curatella* the connective becomes slightly elongated (FIGURE 13). In *Tetracera* the microsporangia may touch apically; however, in other genera they are parallel or basally divergent. At anthesis the partition between adjacent sporangia breaks down and a single chamber is formed. In all genera in the subfamily, dehiscence is always by longitudinal slits. Furthermore, all stamens receive a single, unbranched vascular trace which terminates shortly before reaching the apex of the connective.

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Stamens of the subfamily Dillenioideae show a considerably greater degree of morphological diversity. They are all, nevertheless, fairly well differentiated into filament, anther, and connective and are vascularized by a single trace. In developing stamens two marginally embedded locules are present on each side of the single vascular bundle (FIGURE 21). At anthesis the wall separating adjacent locules disintegrates to form a single chamber. Occasionally raphides may be abundant in the connective.

In *Dillenia* there is an indefinite number of hypogynous, usually free, fertile stamens. Unmodified, partially sterile stamens may also be present (FIGURES 4A, B, C). Staminodia are encountered as free or coherent groups located on the outer side of the androecium, although according to Hoogland (1952) one species (*D. fagifolia*) shows a staminodial cluster on the inner side. Stamens of different species of *Dillenia* may be of equal length, may gradually increase in length centrifugally, or may be sharply separated into groups of different length and shape (FIGURE 19). In the last case, the stamens of the inner group are frequently reflexed abaxially in the bud (FIGURE 4A). The filaments in cross-section are rounded or flattened, some being broader at the base. They vary in length among different species from less than one-fourth to more than one-half the length of the sporangia. The mature anther has four marginal, vertically elongate microsporangia which often become quite protuberant. The connective may project above the sporangia as in *D. papuana* (FIGURE 3). The inner stamens of *D. parviflora* and *D. aurea* have somewhat shorter sporangia located abaxially on the abaxially curving connective (FIGURE 7). Dehiscence is mostly by means of an apical pore but may occur by a longitudinal slit. Hoogland (*loc. cit.*) is of the opinion that this character is of limited taxonomic value.

The stamens of *Acrotrema* vary in number from fifteen to indefinite, usually being located in three groups alternate with the carpels. Hoogland (1951) shows in a diagram the anther of *A. costatum* possessing 2 pairs of elongate, slender microsporangia opening by apical pores, a form comparable to that in species of *Dillenia*. The filaments of *Acrotrema costatum* are comparatively short, whereas those of the Ceylonese plants have long, filiform filaments with two broad, comparatively short sporangia opening by longitudinal slits (FIGURE 10). The sporangia are protuberant and slightly divergent at the base.

The number of stamens in *Hibbertia* varies tremendously from about one hundred fifty to an extreme reduction of only one. Partially sterile stamens and staminodia are also present. The hypogynous stamens are generally arranged surrounding, or alternating with the carpels, but in three sections of the genus they are crowded to one side of the floral receptacle (FIGURE 22). The side of attachment, in axillary flowers, is always away from the main axis so the stamens curve upward in front of the carpels (Wilson, 1965). The androecium of *H. scandens* is composed of stamens with elongate sporangia which are only slightly embedded in the connective. The two pairs of locules are of differing

lengths with the longest opposing pair curving adaxially toward the apex so as almost to touch (FIGURE 9). A contrasting situation is found in *H. dentata* which differs by reduction in length of the sporangia and in the amount of sterile connective tissue (FIGURES 6, 20). Many species have shortened filaments which are broader and basally fused, in varying degrees (FIGURES 8, 12). Dehiscence is by means of longitudinal slits or apical pores.

The fertile stamens of *Pachynema* are ten in number or fewer. Partially sterile stamens and staminodia may alternate with the carpels. The stamens of this genus are very distinctive and differ morphologically from other dilleniaceous species by having a very broad, flattened filament in relation to the anther (FIGURE 11). The anther is narrowed and possesses 2 pairs of marginal, partially embedded sporangia which open by longitudinal slits.

The androecium of *Schumacheria* is unique in its placement at one side of the gynoecium with the large number of stamens united basally by their filaments into an oblique cylindric column. Dehiscence in *S. castaneifolia* is by means of well-defined apical pores. The presence of unicellular, unbranched trichomes is also a feature not found on other Dilleniaceae (FIGURE 5).

Zygomorphy in the androecium is also characteristic of *Didesmandra*. The stamens in this monotypic genus are located in two fascicles. Each staminal cluster is composed of one large, dominant stamen and four smaller ones. The filaments of the four smaller stamens are fused to the filament of the larger one (FIGURE 1) although the veins remain free. Hoogland (1951) refers to the smaller stamens as staminodia but they possess normal sporangia, are vascularized, and produce normal pollen. The marginal, very elongate microsporangia of the dominant stamen are well embedded in the massive connective tissue (FIGURE 23). The stamen is distinctively curved in an uncinate or hooked manner. Dehiscence is longitudinal. The connective extends apically above the sporangia in a deltoid shape. The stamen trace dichotomizes upon entering the projected connective but the resulting branches do not recurve to supply the sporangia.

The following major trends of stamen evolution as recognized by Canright (1952) have occurred within the Dilleniaceae: (1) differentiation of a distinct filament; (2) increase in sporangial size and protuberance with the subsequent transition to a marginal position; and (3) reduction in number of veins from three to one. In addition, there are features generally regarded as indicating androecial advancement restricted to individual taxa: (1) zygomorphy; (2) trichomes occurring on the anther; (3) fusion of filaments; and (4) elongation of the connective. The presence of raphides is a conspicuous feature but of questionable phylogenetic importance.

Even though the stamens of the family are generally of a rather advanced type, when considered as a whole, a greater number of unspecialized stamen features occur in the subfamily Dillenioideae. Evidence

of this is seen in the retention of elongate sporangia, rather broad filaments, and the presence in some species of relatively large amounts of sterile tissue. Although there is no dilleniaceous stamen which resembles the primitive, three-trace, ranalian microsporophyll, there is little difficulty in visualizing evolution from such a primitive type.

YOUNG STEM

Since a reasonably complete account of dilleniaceous stem anatomy may be found in Solereder (1908) and Metcalfe and Chalk (1950), the following statements are merely intended to verify these treatments and in some instances make them more comprehensive.

Stems are cylindrical or distinctly lobed (FIGURE 27), flattened in *Pachynema dilatatum*, and rhizomatous in *Acrotrema*. Secondary vascular tissue produced only in limited amounts in *Acrotrema* and *Pachynema* (FIGURE 28). NODES trilacunar in species of *Acrotrema*, *Doliocarpus*, *Hibbertia* and *Tetracera*; multilacunar in *Curatella*, *Davilla*, *Didesmandra*, *Dillenia*, *Doliocarpus* and *Schumacheria*; unilacunar by reduction in species of *Hibbertia*. TRICHOMES, when present, of the same type and occurrence as reported for leaves (Dickison, 1970). PERIDERM originating in the innermost layers of the cortex in *Curatella* (FIGURE 25), *Davilla*, *Doliocarpus* (FIGURE 27), *Hibbertia*, and *Tetracera*; subepidermal in *Dillenia* and also apparently in *Doliocarpus dentatus*. CORTEX and PITH composed of large, thin-walled parenchyma in *Didesmandra* (FIGURE 24), *Acrotrema*, *Schumacheria*, and species of *Dillenia*, *Hibbertia*, and *Tetracera*. Greatly enlarged idioblastic pith cells observed in *Davilla aspera*. Pith and cortical cells often thick-walled and sclerotized in other taxa. The narrow cortex of *Didesmandra*, as seen in FIGURE 24, is distinctive of the species. Dark staining mucilage (tannin?) cells and raphides are characteristic for the family. Thick-walled cortical sclereids and fibers are frequently abundant in *Curatella* (FIGURE 25), *Davilla*, *Doliocarpus*, *Tetracera*, and are especially conspicuous in *Pachynema* (FIGURE 28). VASCULAR BUNDLES collateral and initially separate (FIGURES 24, 26), but as a result of cambial activity the stele becomes complete very early in *Acrotrema*, *Doliocarpus*, *Hibbertia*, *Pachynema*, and species of *Tetracera*. In all species investigated the primary xylem consisted of spiral to scalariform tracheary elements.

PHLOEM

Literature dealing with phloem anatomy of the Dilleniaceae is extremely meager. The development of the sieve plate in *Tetracera* sp. has been discussed by Esau and Cheadle (1965) while Zahur (1959) described the phloem anatomy of a single unnamed species of *Saurauia* but did not consider any members of the Dilleniaceae *sensu stricto*.

To facilitate comparisons, the sieve tube classification utilized by Zahur (*loc. cit.*) is followed. This system categorizes elements into three types: (I) sieve tube elements long with very oblique sieve plates con-

taining ten or more sieve areas, (II) sieve tube elements of medium length with oblique sieve plates containing two to ten sieve areas, and (III) sieve tube elements short with slightly oblique to transverse, simple plates.

The late metaphloem and early secondary phloem is uniformly characterized by the presence of sieve tube members, companion cells, and scattered crystal-bearing parenchyma cells (FIGURE 29). In most species, phloem parenchyma and ray cells are filled with an abundance of dark-staining, tannin-like material (FIGURE 32). In the secondary phloem, sieve tube elements tend to be radially aligned. Abundant perivascular fibers and sclereids were observed in all taxa except *Acrotrema* sp., *Didesmandra*, species of *Hibbertia* (*H. cuneiformis*, *H. dentata*, *H. scandens*, *H. tetrandra*), *Dillenia indica*, and species of *Tetracera* (*T. indica*, *T. macrophylla*, *T. scandens*) where they are absent or weakly developed. Sclerenchyma is never present in the phloem proper. The absence of perivascular sclerenchyma in the stem is generally correlated with the absence of vein sheathing in the leaf.

Sieve tube elements in *Didesmandra* (FIGURE 32) and *Schumacheria* (FIGURE 36) are prevailingly Type III. The simple sieve plates are transversely oriented or only slightly oblique. *Davilla*, *Curatella* (FIGURE 33), *Hibbertia* (FIGURE 35), and *Tetracera* (FIGURE 34) possess Type II elements with an occasional Type III (FIGURE 30). In these genera the sieve plates vary from transverse to oblique with compound sieve plates composed of two to five (rarely more) sieve areas. *Dillenia* also contains almost exclusively Type II elements although *D. indica* (FIGURE 31) showed a number of elements with very oblique, compound sieve plates containing up to ten sieve areas, thus approaching Type I. Diffuse lateral sieve areas are quite distinct on the elements of *Hibbertia* (FIGURE 35), *Dillenia*, and *Didesmandra*. Sieve plate pores are generally less than 1 μ in diameter and are lined with a layer of callose (FIGURE 30). Although statistical data were not gathered, preliminary measurements indicated sieve tube elements in all genera were usually short (less than 300 μ). It should be noted that phloem of a climbing member of the family was not examined; however, sieve tube elements often become structurally modified in response to this habit.

Although suggested trends of phylogenetic specialization for the phloem of dicotyledons (see Esau, 1965) have not been demonstrated to be either unidirectional or irreversible, the following major evolutionary trends in sieve tube elements have been proposed and are widely accepted by plant anatomists: (1) localization of specialized sieve areas on the end walls, (2) change in orientation of end walls from very oblique to transverse, and (3) progressive change from compound to simple sieve plates. The significance of sieve tube element length and lateral sieve areas is still a matter of controversy. For a more detailed discussion the reader is referred to Zahur (*loc. cit.*) and Carlquist (1961).

In view of the above conclusions, it is interesting to compare the relative advancement of the phloem of the Dilleniaceae with other structures

of the plant. Although the wood anatomy of the subfamily Dillenioideae is comparatively primitive, the phloem is not at a similar low level of specialization. No dilleniaceous genus possesses exclusively Type I sieve tube elements. Moreover, the vessel members of *Didesmandra* and *Schumacheria* are very unspecialized, whereas their sieve tube elements with simple, transverse sieve plates are very advanced. Similarly, *Curatella* and *Davilla* with rather advanced wood have a less specialized phloem. The fact that organs and structures do not evolve at the same rate within an individual plant has been demonstrated numerous times in the Dilleniaceae. Phloem anatomy alone does not suggest that the family Dilleniaceae is a particularly primitive one.

DISCUSSION

Comprehensive anatomical investigation has disclosed that the Dilleniaceae are significantly more variable in morphology than has previously been suspected. Moreover, it is evident that the lack of study on many dilleniaceous species, notably New World forms, resulted in most family descriptions being based on Old World genera, particularly *Dillenia* and *Hibbertia*. There is, accordingly, little question of why erroneous alliances and concepts were established from past considerations. Although it is difficult to find a single outstanding character which clearly distinguishes Dilleniaceae from related taxa, the ten genera comprising the family (*sensu* Hoogland, 1951) form a natural group despite their obvious differences in habit (trees, shrubs, lianas, rhizomatous herbs). This is reflected in both floral and vegetative characters, in addition to the presence of an unusually large number of well-defined evolutionary trends (see previous papers in this series, Dickison 1967a, b, 1968, 1969, 1970a). In many instances vegetative trends can be directly correlated with extremes, or historical changes, in the habitat and/or habit of the plant, thus leaving little doubt as to the direction the specialization has taken. Trends in other parts of the plant, however, may only be interpreted as indicating phylogenetic advancement. Although these facets cannot always be sharply separated, further ecological study assessing the modifying influence of the environment, in both individual plants and groups of related plants in different geographic areas of the world, would be rewarding and is worthy of future study. The large number of these specializations, therefore, makes the family of more than usual phylogenetic and ecological interest.

The genera *Actinidia* and *Saurauia*, included in the Dilleniaceae by Gilg (1893), are now generally removed and assigned to their own distinct family (or families), or else placed in one or more already established families. The exact relationship of these two genera to the Dilleniaceae and to one another is currently under study and will be the subject of forthcoming papers.

Intrafamilial Relationships. Nearly all intrafamilial classifications of the Dilleniaceae are based exclusively, or partially, on stamen struc-

ture. The contemporary system of Hoogland (1952, 1953) divides the family into two subfamilies, the Dillenioideae and Tetraceroideae, with the latter group characterized primarily by the broadened and sometimes thickened stamen connective. It seems doubtful that this often unreliable character alone is sufficient basis for separation of two large groups; however, when coupled with the totality of anatomical and morphological evidence obtained elsewhere in the plant (e.g., wood anatomy) the family is readily divisible into two subfamilies. Data derived from phytochemistry is also compatible with this treatment (Kubitzki, 1968). It should be noted, however, that there is considerable overlapping in characters of possible taxonomic importance.

Of the two subfamilies, the Dillenioideae retain a larger number of primitive characters (as regards wood anatomy, carpels, stamens). It should be emphasized in this connection that neither subfamily retains all the more primitive or all the more advanced features. As is so often the case in dicotyledonous families, dilleniaceous genera usually possess a combination of primitive and advanced features.

The more numerous, more diversified, and exclusively Old World subfamily Dillenioideae includes the genera *Acrotrema, Didesmandra, Dillenia, Hibbertia, Schumacheria* and *Pachynema*. Its distribution is characterized by a comparatively high number of endemics containing few species. For example, *Acrotrema* is confined to Ceylon with the exception of one species (*A. arnottianum*) in southern India and one species (*A. costatum*) in Thailand and Malaysia. The monotypic *Didesmandra* is currently known from only a single collecting site in Sarawak, Malaysia. *Schumacheria*, with two or three species, is confined to Ceylon, while *Pachynema*, with about five species, is known only from interior Australia. In contrast, *Dillenia* is a fairly large genus with about sixty species and has a distribution ranging from Madagascar to Fiji. The genus ranges northward to the southern Himalayan slopes, Yunnan and Hainan Islands, and in a southern direction to the east coast of northern Queensland, Australia. The largest genus in the family, *Hibbertia*, with about one hundred species, is distributed principally in Australia but extends from Madagascar to Fiji.

Ozenda (1949) concluded after his study of the Dilleniaceae that the tribes Hibbertieae and Tetracereae (*sensu* Gilg & Werdermann, 1925) were more advanced than, and presumably derived from, the tribe Dillenieae. This concept was formulated on the basis that the Dillenieae possess multilacunar nodes, which Ozenda considered the primitive pattern. I do not find this treatment satisfactory.

Hoogland (1952) observed that the genera within his subfamily Dillenioideae showed reticulate relationships and could be arranged in different ways according to the principals employed. Data derived from comparative morphology is more in keeping with this idea. In my opinion, the ancestor of this very old group is extinct, the extant genera having been separated for so long a period that their affinities are now

obscured. Nevertheless, certain generic relationships and levels of evolutionary advancement may be discussed.

The genus *Hibbertia* includes species with the largest number of primitive features, viz., completely actinomorphic flowers, an androecium composed of an indefinite number of uniform stamens with elongate microsporangia, an apocarpus gynoecium with open, conduplicate, three-veined carpels containing numerous ovules, primitive wood containing vessel elements with exclusively scalariform perforation plates, trilacunar nodes, sieve tube elements with oblique, compound sieve plates, and reticulated, tricolpate pollen. (The trends in pollen morphology of the Dilleniaceae which I have already tentatively suggested, have been strengthened by the recent paper on Cretaceous angiosperm pollen by Doyle, 1969.) Within this same large, highly diversified genus, however, occur some of the most specialized (often reduced) species in the family.

The fact that all other dilleniaceous genera could not have been derived directly from any extant hibbertias is substantiated by the more primitive wood anatomy (i.e., vessel elements) of *Didesmandra* and *Schumacheria*. It is interesting to note both genera are shrubs or small trees. Although the wood of these two related genera is the least advanced in the family, their floral morphology, tetracolpate pollen, nodal anatomy, and sieve tube elements are indicative of advancement.

That *Dillenia* should not be relegated to the primitive position in the group is made clear by the syncarpous gynoecium on a conical receptacle, by the multilacunar nodes, the comparatively more advanced wood structure, and the occasionally porate pollen. Phytochemistry also supports a more advanced position (Kubitzki, 1968). The significance of petiolar wings is uncertain although Meeuse (1966, p. 203) believes they are the forerunners of stipules. *Pachynema* appears to be a very specialized offshoot of *Hibbertia* while the rhizomatous, herbaceous *Acrotrema* is probably distantly related to *Dillenia*.

The subfamily Tetraceroideae is made up of the New World genera *Curatella*, *Davilla*, and *Doliocarpus*, as well as the pantropical *Tetracera*. The largest number of species is found in the Amazon region of Brazil, but the range extends from Peru, central Bolivia, and northern Paraguay northward into Mexico. The monotypic *Curatella* grows the farthest north having been collected from Tepic eastward to Vera Cruz. These genera also range throughout the West Indies and Cuba. *Tetracera* is pantropical with the exception of the Pacific islands east of New Britain and New Caledonia, and is therefore, the only dilleniaceous genus to occur in Africa.

As stated previously, this subfamily is more advanced *as a whole* than the Dillenioideae. *Tetracera* with an androecium of indefinite stamens, apocarpous gynoecium, and trilacunar nodes is the least advanced genus, although wood anatomy and the unisexuality of New World species is quite specialized. *Curatella*, *Davilla*, and *Doliocarpus* are the most highly evolved genera in the family making it impossible to derive one genus from any other.

The next pertinent question is, where did the family originate and how did it attain its present distribution? With regard to the first question there seems to be little doubt that the family Dilleniaceae had its origin in the Indomalayan-Australasian tropics, with a subsequent migration to present localities. Following the criteria outlined by A. C. Smith (1967), the evidence for this conclusion is as follows: (1) there are more genera and species represented in the Old World than in the New World, (2) the family is considerably more variable in the Old World in comparison to the New World, and (3) the New World species are comparatively more highly evolved than the Old World species. The similarity of the Dilleniaceae in these respects to other primitive angiospermous families is striking (see Smith, *loc. cit.*).

The present distribution of the Dilleniaceae has been explained in one manner by Willis (1907). According to him the problem becomes simple if one assumes the former existence of the continent Brazilia-Ethiopica linking Africa and South America, with land connections to Ceylon and Malaya. This author reasoned that since *Tetracera* appeared to be comparatively primitive morphologically, and is, in general, widely distributed, it was probably the first dilleniaceous genus to arise in the Brazilia-Ethiopic land mass. From this origin, the family radiated to South America, Africa, Ceylon, Malaya, and lastly, from Malaya to Australia. Although this idea may be convenient, it is nevertheless highly theoretical and not at all supported by evidence from comparative morphology and elsewhere.

The fossil record of the Dilleniaceae is, unfortunately, most incomplete and what has been described is somewhat dubious. Berry (1916, 1925) reported specimens of *Dillenites* from the Ripley Formation (Upper Cretaceous) and Wilcox Flora (Lower Eocene) of North America. If these leaf impressions are in fact Dilleniaceae, it illustrates the wider range of the family during the Tertiary, as was common in other dicot families, but does not shed substantial light on possible migration patterns. For the most part, the widely distributed nature of extant genera leaves the question of migration routes unanswered.

Place of Dilleniaceae in the general system. The much followed system of Gilg (1893), in Engler and Prantl's *Die natürlichen Pflanzenfamilien*, placed the Dilleniaceae in association with the Sterculiaceae and Eucryphiaceae in the large order Parietales. The artificiality of this treatment has been demonstated by comparative wood anatomy and pollen morphology (Dickison, 1967a, b). Lawrence (1951, p. 598), in commenting on the Dilleniaceae states, "Evidence is accumulating to establish the family as much more primitive than was allowed by Engler, and it is probable that its alliance is with or near the ranalian taxa."

Most early workers (e.g., Bentham & Hooker, 1862; Bessey, 1915), in fact, believed the family exhibited features which justified its inclusion with the Ranales (i.e., Magnoliales, Annonales). For the most part, these decisions were prompted by considerations from floral morphology, viz., polypetalous corolla, apocarpous gynoecium, numerous stamens, etc.,

as well as the persistent calyx and presence of an aril on the seed. From the extensive anatomical information obtained on the ranalian families by Bailey and co-workers, it can now be established that if the Dilleniaceae were to have affinities with the ranalian complex, it is manifest that such relationships lie with those families possessing (1) true vessels, (2) tri- or multilacunar nodes, (3) tricolpate or derived pollen, (4) well differentiated, one-trace stamens, (5) one-trace petals, and (6) no "ethereal oil cells." The number of ranalian families sharing this combination of rather advanced characters becomes considerably reduced. The presence or absence of any one of these features in other ranalian families is sufficient basis to preclude a close association. It is now clear from this series of studies, that the Dilleniaceae are not anatomically comparable to any specific ranalian family. Kubitzki (1968), furthermore, notes the Dilleniaceae share the capacity of producing trihydroxylated compounds with various families of the Cistiflorae and Rosiflorae but differ greatly from the Polycarpicae (Ranales) in this respect.

The Ranales (*sensu lato*) have often been regarded as a heterogeneous assemblage and a repository for plants retaining primitive characters in one or more of their organs (Swamy & Bailey, 1949). The Dilleniaceae, in part, retain such primitive characters in wood anatomy, floral morphology, and seed structure (with abundant endosperm and small embryo). In addition, according to Wilson (1965), the stamen trunk is a primitive feature while the DURIAN THEORY of Corner (1949a, 1954b) assumes that the seeds of ancient angiosperms were arillate, as in the dillenias. Nevertheless, the *totality* of anatomical-morphological data indicates the family *as a whole* is more highly evolved. In view of this evidence, I believe nothing would be gained by including the Dilleniaceae in the ranalian complex, except to make the complex still more heterogeneous.

From the preceding discussion it is clear that I (and most other workers) do not believe the Dilleniaceae represent the most primitive living angiosperms. This opinion is sharply opposed to that of Meeuse (1966, p. 204, 205) who contends that the Magnoliales do not represent primitive angiosperm types, but he attributes to his theoretical basic group characters which suggest that the Dilleniaceae, "are apparently not very far advanced beyond this deduced ancestral stage . . . ." According to the prevailing concepts of angiosperm morphology this is not the case.

Hutchinson (1926) was the first to raise the family to ordinal rank; a position I believe justified on anatomical grounds. Within his Dilleniales he brought together the Dilleniaceae and Crossosomataceae. A later edition (Hutchinson, 1959) follows basically the same treatment except that the Brunelliaceae and Connaraceae enter the association. The placing the latter two families near the Dilleniaceae is questionable and needs future study. In this system, the Dilleniales is a supposed connecting link between the remotely related Magnoliales and such groups as Rosales, Bixales, Theales, and Guttiferales.

In 1950, Camp suggested the genus *Paeonia* (Paeoniaceae) was related to the Dilleniaceae, an association which has subsequently gained support from floral anatomy and morphology (Eames, 1953), and is now rather prevalent. The resulting three family complex — Dilleniaceae, Paeoniaceae, and Crossosomataceae — has been generally widely accepted. Cronquist (1957, 1965) placed these families under the Dilleniales but noted the association was not firmly established and the sequence of stamen development was the only essential character by which the Dilleniales differed from the Ranales. The following features characterize the Dilleniales according to Cronquist (1968): (1) persistent, imbricate sepals, (2) numerous, centrifugal stamens, (3) binucleate pollen, (4) apocarpous gynoecium, and (5) bitegmic, crassinucleate ovules which mature into arillate seeds with abundant endosperm. The order differs from the Theales only in that the latter possesses a syncarpous gynoecium. Eames (1961) further characterizes the group as having a fasciculate arrangement of the stamens which in his view supports the idea that the Dilleniales represent the ancestral stock for the Guttiferae and related families. This same conclusion has been reached by Decker (1966) from wood anatomy, and most recently by Schofield (1968) on the basis of nodal and petiolar anatomy. It should be kept in mind, however, that neither an apocarpous gynoecium nor arillate seeds is a uniform feature of all Dilleniaceae. Also, a centrifugal androecium has been reported for only three dilleniaceous genera.

Cronquist (*loc. cit.*) considers the Dilleniales derived directly from the closely related Magnoliales and ancestral to the Theales (Guttiferales) and the remainder of his subclass Dilleniidae. Of particular note in this system is the fact that the Rosales are not considered to be related to the Dilleniaceae but rather to have their origin directly from the Magnoliales. This is still a matter of debate. The differences in carpel vascularization between the Dilleniaceae and Rosaceae (Dickison, 1968) appear noteworthy.

The relationship of *Paeonia*, but not *Crossosoma*, to the Dilleniaceae has been supported by Zamora (1965). In an effort to determine the trends of specialization in primary xylem structure, he has shown that the perforation plate transition in the protoxylem-metaxylem elements of *Paeonia* is similar to that in *Dillenia* and *Tetracera*, whereas the primary xylem structure of *Crossosoma* differs from both the Paeoniaceae and Dilleniaceae. The presence in the secondary xylem of *Crossosoma* of vessel elements with exclusively simple perforation plates should again be emphasized. The serious lack of accurate anatomical data for the Crossosomataceae is evident and currently prevents critical comparisons. All available evidence indicates that *Crossosoma* is a rather isolated genus. However, the recent study on this group by Dr. P. E. Richardson (1968) should shed some much needed light.

Thorne (1968) has chosen to relate the Dilleniaceae and Paeoniaceae but places *Crossosoma*, perhaps correctly, near the Rosaceae. He also prefers to put the dillenias and *Paeonia* under a broad concept of the

Theales. In a similar fashion, Melchior (1964) places the group in the suborder Dilleniineae of the expanded Guttiferales (incl. Theales). It seems to me this makes for very large, heterogeneous associations and implies a closer affinity between the Dilleniaceae and Theaceae than actually exists. The syncarpous gynoecium, unilacunar nodes, and occasionally versatile anthers, as well as the embryology of the Theaceae are quite distinctive.

It is readily apparent that the presence of centrifugal stamen development is of central importance in all discussions pertaining to the dilleniaceous complex. Although the phenomenon was first reported by Payer (1857), it was Corner (1946) who fully developed its taxonomic and phylogenetic significance. It was his thought that those families which possess centrifugal androecium development, as compared with the more common centripetal pattern, represent a natural alliance well apart from the ranalian line. In view of the importance ascribed to this character, it is surprising to note how poorly understood it is. Hoogland (1952) observed that Corner studied a flower of a species (*Dillenia suffruticosa*) in which the stamens gradually diminish in size centrifugally. He suggested the investigation be repeated in a species where the stamens of the open flower are about equal in size. Hiepko (1965) after a developmental study on the flower of *Paeonia* concluded that the term "centrifugal androecium" should refer only to the origin of stamens developmentally and not to their sequence of maturation. On this basis he was unable to confirm the occurrence of the centrifugal character in the Theaceae or Winteraceae. The only study of the Dilleniaceae in this manner has been that of Sattler (1968) on *Hibbertia scandens*. Other genera of the family undoubtedly need investigation.

In conclusion, it is my opinion that retention of the order Dilleniales is the most satisfactory treatment. The composition of the order still needs clear definition. The family Dilleniaceae would appear to be an extremely old one. Although some species retain vestiges of primitiveness, the major part of the family has become rather highly evolved. If the family originated from Magnolialian stock, this must have occurred very early in the evolution of both groups. At our present state of knowledge, all evidence indicates that the family gave rise to the Guttiferales and Theales.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–17. Stamen morphology of Dilleniaceae. All figures drawn from cleared specimens. FIG. 1, *Didesmandra aspera*, only one smaller stamen is shown. FIG. 2, *Dillenia indica*. FIG. 3, *D. papuana*. FIG. 4A, *D. alata*, inner, recurved stamen; B, outer stamen; C, staminodia. FIG. 5, *Schumacheria castaneifolia*. FIG. 6, *Hibbertia dentata*. FIG. 7, *Dillenia parviflora*. FIG. 8, *Hibbertia exutiacies*. FIG. 9, *H. scandens*. FIG. 10, *Acrotrema* sp. FIG. 11, *Pachynema dilatatum*. FIG. 12, *Hibbertia tetrandra*. FIG. 13, *Curatella americana*. FIG. 14, *Doliocarpus dentatus*. FIG. 15, *Davilla aspera*. FIG. 16, *Tetracera indica*. FIG. 17, *T. volubilis*.

PLATE II

FIGS. 18–23. Stamen morphology of Dilleniaceae, continued. FIG. 18, *Doliocarpus dentatus* (*Krukoff 10407*), cleared stamen showing single trace (st) and abundant raphides (r) in connective, × 70. FIG. 19, *Dillenia ovata* (*Cult.* SING *s.n.*), transverse section through floral bud with perianth parts removed showing distinct grouping of androecium into outer (os) and inner (is) stamens, × 26. FIG. 20, *Hibbertia dentata* (*Cult.* K *s.n.*), transverse section of anther showing longitudinal dehiscence and slender connective, × 64. FIG. 21, *Dillenia philippinensis* (*J. V. Pancho s.n.*, from Makiling, Philippines), transverse section of stamen prior to anthesis and disintegration of wall separating the two locules on each side of the single stamen trace (st), × 65. FIG. 22, *Hibbertia exutiacies* (*Eichler 17965*), transverse section through flower showing oblique carpels, and stamens inserted at one side of gynoecium, × 27. FIG. 23, *Didesmandra aspera* (SAR *18297*), transverse section through stamen showing massive connective, marginally embedded sporangia, and longitudinal dehiscence, × 26.

PLATE III

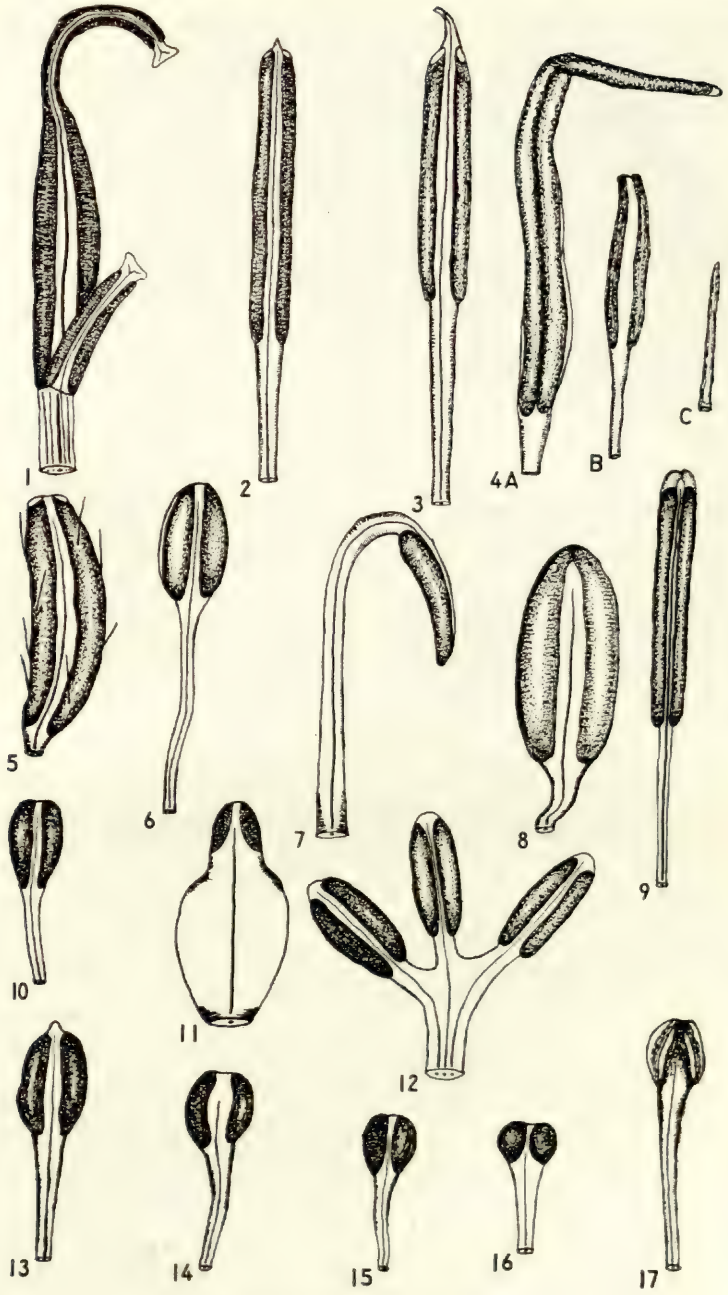
FIGS. 24–29. Stem anatomy of Dilleniaceae. All figures × 33 except FIGURE 29, × 81. FIG. 24, *Didesmandra aspera* (preserved material from Sarawak, *s.n.*), transverse section of young stem showing isolated vascular bundles, narrow cortex, large, thin-walled pith, and cortical parenchyma (note absence of sclerenchyma). FIG. 25, *Curatella americana* (*H. S. Irwin 5470*), transverse section illustrating origin of periderm (p) in the inner cortex, and abundant cortical sclereids (scl). FIG. 26, *Schumacheria castaneifolia* (preserved material from Waga, Ceylon *s.n.*), transverse section showing separate vascular bundles and weakly developed perivascular sclerenchyma. FIG. 27, *Doliocarpus major* (*I. M. Johnston 1694*), transverse section of older stem showing continuous vascular cylinder and origin of periderm in the inner cortex. FIG. 28, *Pachynema junceum* (NT *6750*), transverse section through mature stem illustrating limited secondary growth and abundant, thick-walled fibers in cortex. FIG. 29, *Dillenia excelsa* (preserved material from Malaya, *s.n.*), transverse section through secondary phloem showing radially aligned sieve tube elements (s) with associated companion cells (cc), enlarged crystal-containing parenchyma (cr) and perivascular sclerenchyma (scl). Note characteristic dark-staining contents of the phloem rays.

PLATE IV

FIGS. 30–36. Phloem anatomy in stems of Dilleniaceae. FIG. 30, *Hibbertia dentata* (*Cult.* K *s.n.*), transverse view of simple sieve plate, × 1600. FIG. 31, *Dillenia indica* (*Cult.* BRI *s.n.*), longitudinal view of oblique, compound sieve

plate, × 650. FIG. 32, *Didesmandra aspera* (preserved material from Sarawak *s.n.*), transverse section of simple sieve plate, × 650. FIG. 33, *Curatella americana* (*H. S. Irwin 5470*), transverse section of slightly oblique, compound sieve plate, × 1600. FIG. 34, *Tetracera indica* (preserved material from H. Keng, *s.n.*), longitudinal section showing oblique, compound sieve plate, × 670. FIG. 35, *Hibbertia scandens* (*Cult.* K *s.n.*), longitudinal section of sieve tube element illustrating oblique sieve plate and lateral sieve areas, × 650. FIG. 36, *Schumacheria castaneifolia* (preserved material from Waga, Ceylon *s.n.*), longitudinal view showing sieve tube elements with transverse sieve plates and dark staining phloem parenchyma, × 300.

Explanation of symbols: pp, phloem parenchyma; s, sieve tube member, sa, sieve area; sp. sieve plate.



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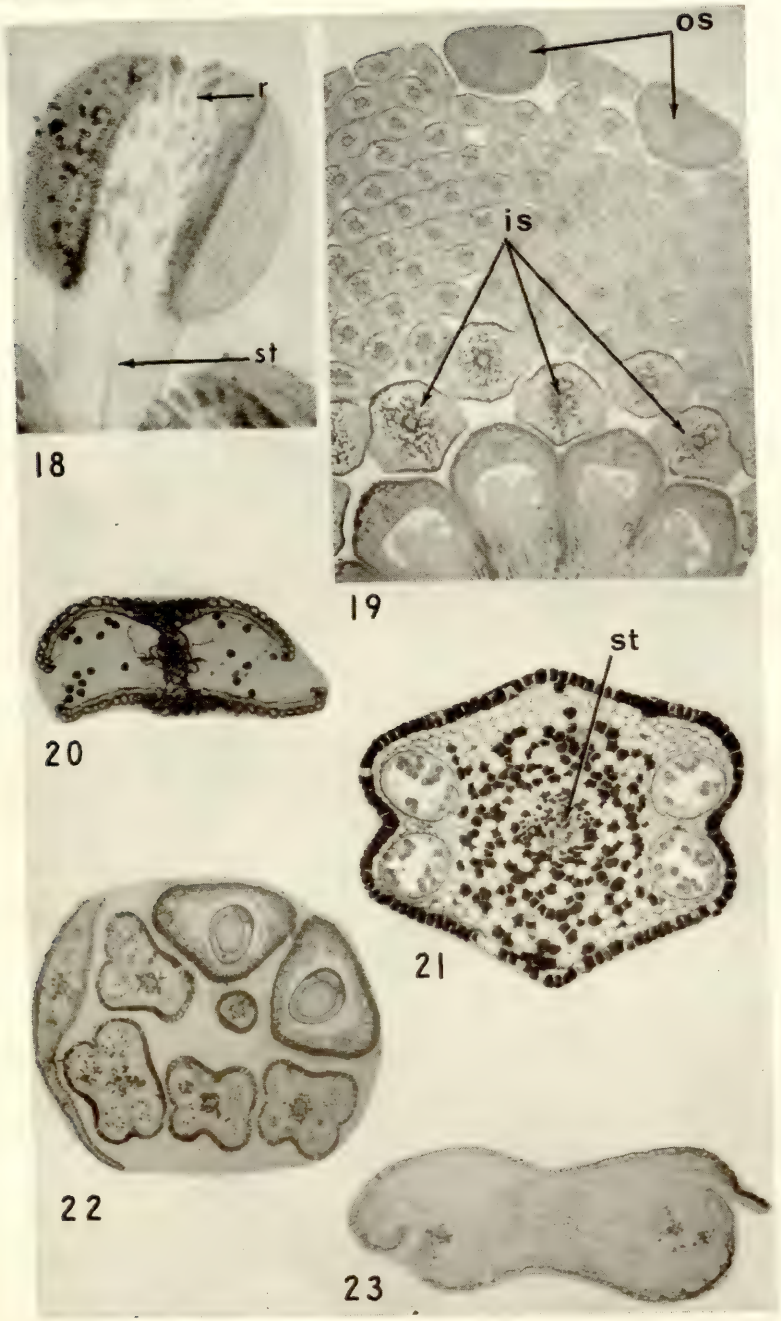

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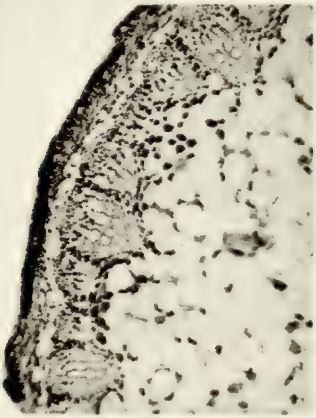

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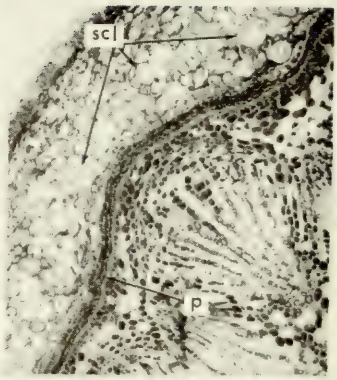

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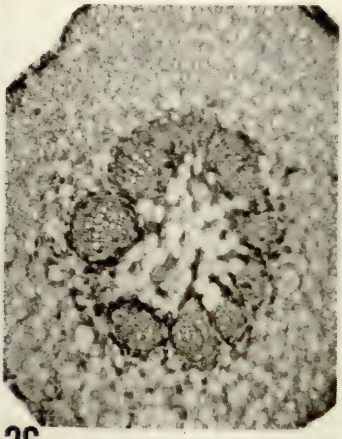

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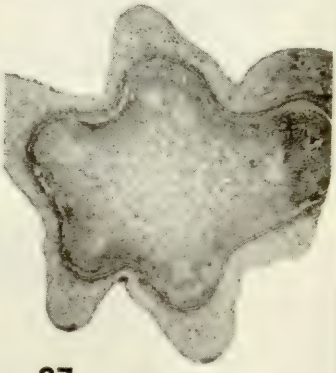

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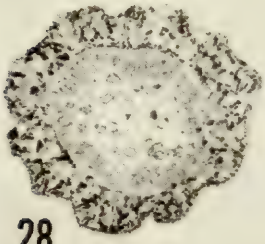

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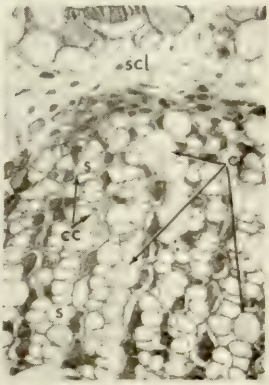

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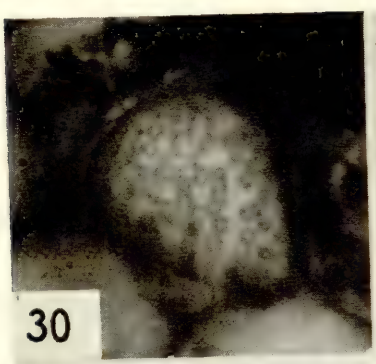
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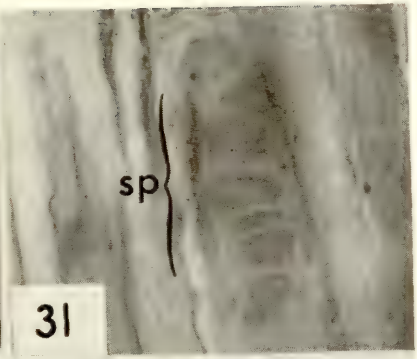
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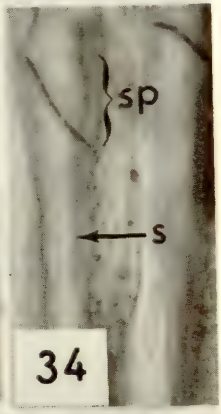
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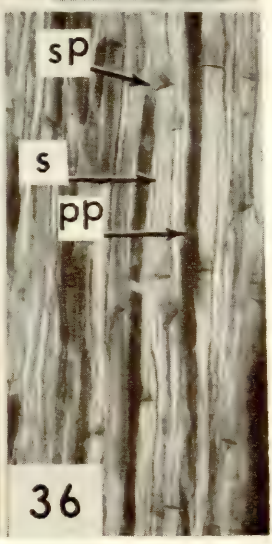
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ADDITIONAL NOTES ON THE MALESIAN SPECIES OF ZANTHOXYLUM (RUTACEAE)

THOMAS G. HARTLEY

SINCE THE PUBLICATION of my revision of the Malesian species of *Zanthoxylum* (Jour. Arnold Arb. 47: 171–221. 1966) I have examined a considerable number of additional Malesian collections of that genus. As a result, the descriptions of some of the species should be amplified and several range extensions may be reported. Also, it has come to my attention that one of the names used, *Z. limonella* (Dennst.) Alston, is invalid, and, accordingly, the necessary correction is made.

The species are numbered here in the same order as in the revision. Only those collections pertinent to the comments are cited in full. However, a complete list of all additional numbered collections examined is included as a supplement to the original Index to Exsiccatae.

Grateful acknowledgment is made to the directors and curators of the Herbarium Bogoriense, Djalan Raya, Bogor, Indonesia (BO) and the Rijksherbarium, Leiden (L), for the loan of herbarium specimens. Benjamin C. Stone, of the University of Malaya, Kuala Lumpur, is also thanked for sending a duplicate of his recent collection of *Zanthoxylum acanthopodium* from Malaya.

2. Zanthoxylum nitidum (Roxb.) DC.

The range of this species may be extended to include the Philippine island of Mindanao.

Philippines. MINDANAO: Lake Lanao, *Clemens*, May 1907 ♀ (BO).

5. Zanthoxylum avicennae (Lam.) DC.

The range of this species may be extended to include the Celebes. Also, it is now confirmed that the collection cited for the provisional name *Fagara anisata* Back. ex Bakh. f. (*Backer 11431*) is *Zanthoxylum avicennae*.

Java. EAST JAVA. Kediri, G. Wilis, *Backer 11431* 2 sheets, ♂ and ♀ (BO). **Celebes.** Res. Manado, Paloe, *NIFS bb 3* ♀ (BO), *Pesik NIFS bb 9* (BO).

6. Zanthoxylum megistophyllum (Burtt) Hartley

With the addition of the recent Bougainville collections of R. Schodde and L. Craven the description of this species may be amplified somewhat. Also, the range may be extended slightly to include Santa Ysabel Island in the Solomons.

Small to medium trees to 17 m. Inflorescences to 44 cm. long. Anthers

of staminate flowers 0.5–1 mm. long. In primary and secondary rain forests at altitudes up to 690 meters.

Solomon Islands. BOUGAINVILLE: Near Koniguru No. 1, ca. 10 miles N of Buin, *Craven & Schodde 107* ♂ (L); Lake Laloru Crater, ca. 14 miles N of Buin, *Craven & Schodde 260* ♂ (L); vicinity of Aku, ca. 9 miles W of Buin, *Schodde & Craven 4110* ♂ (L). SANTA YSABEL: Moloforu Bay, *Beer's Collectors BSIP 7376* ♀ (L).

7. Zanthoxylum forbesii Hartley

The original description of this species was based on a single fruiting collection from Sumatra. With the addition of a staminate flowering specimen from Sumatra and a fruiting specimen from Java, the description and range may be amplified as follows:

Small (4 m.) to large trees; dioecious. Leaves paripinnate or imparipinnate, glabrous, 40–70 cm. long; petiolules of lateral leaflets 0.6–1 cm. long; leaflets with 12–19 veins on each side of the midrib, 15–27 cm. long, 5–10 cm. wide, obtuse to acutely oblique at base, short to rather long acuminate at apex, the acumen to 1.7 cm. long. Inflorescence terminal, paniculate, 24 cm. long and about half as broad, the axes and branches glabrous. Staminate flowers (in bud) 3 mm. long; pedicels 1 mm. long; sepals 4, green, broadly triangular, 1 mm. long, connate at about half their length; petals 4, white, elliptic, 2.5 mm. long; stamens 4, filaments 1 mm. long, anthers 2 mm. long; disc pulvinate, about 0.5 mm. high; rudimentary carpels 2, about 0.5 mm. high.

Sumatra. Padangsidimpoean, *Kostermans 22042* ♂ (L). **Java.** WEST JAVA. Tokoka, *Koorders 6983* ♀ (BO).

9. Zanthoxylum retroflexum Hartley

A second collection of this species has leaves ascending rather than sharply reflexed as in the type collection. This necessitates deleting each of the first statements in the 7th couplet of the key (p. 176) and altering the description to read, with regard to the leaves: "... ascendentibus vel acute reflexis, ..." Field studies are desirable to determine what factors are involved with the reflex movement of the leaves in this species.

Sumatra. Palembang District, Tjabang Forest Res., *Kostermans S 42* ♀ (L).

10. Zanthoxylum rhetsa (Roxb.) DC.

The name used in the revision, *Zanthoxylum limonella* (Dennst.) Alston, is invalid since the basionym, *Tipalia limonella* Dennst., represents a combined new generic name and specific epithet listed with only a reference to a plate and description in *Hortus Indicus Malabaricus*. Rickett and Stafleu (Taxon 10: 80. 1961) have pointed out that such names in Dennstedt's publication are *nomina nuda* because new generic and specific combinations cannot be validated by reference to a previous publication. Details of Dennstedt's *Schlussel zum Hortus Indicus Malabaricus* with

lists of the valid and invalid names were given recently in a paper by H. Manitz (Taxon 17: 496–501. 1968).

The choice of the name *Zanthoxylum rhetsa* over *Z. budrunga* (Roxb.) DC., the basionyms of which were published on the same date, follows Hooker f., Fl. Brit. India 1: 495. 1875.

The range of this species may be extended to include Madoera Island, just north of Java, and the islands of Bali and Timor.

Java. Madoera Island, N. van Soemenep, *Backer 20669* (BO). **Lesser Sunda Islands.** BALI: *Becking 49* (BO), *70* (BO). TIMOR: N Midden Timor, *NIFS bb 7223* (BO).

14. Zanthoxylum pluviatile Hartley

A recent collection by J. S. Womersley from near the type locality is the first carpellate flowering material I have seen of this species. The description of the flowers follows. Also, the range may be extended to include New Britain, apparently the first *Zanthoxylum* ever collected from that large island, and to another of the Solomon Islands, Malaita Island.

Carpellate flowers 4–5 mm. long; pedicels, sepals and petals as in staminate flowers; rudimentary stamens 0.2 mm. long; disc subpulvinate, about as thick as the base of the ovary, 0.75 mm. high; gynoecium 1-carpellate, 2 mm. high, style excentric, stigma flattened.

Territory of New Guinea. MOROBE DISTRICT: Markham River logging area, *Womersley NGF 19198* ♀ (L). **New Britain.** Kandrian Subdistrict, Pulie River, *Henty & Frodin NGF 27243* ♂ (L). **Solomon Islands.** Malaita Island, Dala, *Snyder BSIP 4477* (L).

16. Zanthoxylum integrifoliolum (Merr.) Merr.

The following collection documents the report of this species from Taiwan:

Taiwan. Lanyu Island (Botel Tobago), *Chang 3136* ♀ (L).

17. Zanthoxylum ovalifolium Wight

The range of this species may be extended to include Borneo.

Indonesian Borneo (Kalimantan). Martapoera, *Daoen Limauan NIFS bb 568* ♀ (BO).

18. Zanthoxylum acanthopodium DC.

This species was recently reported from Malaya by B. C. Stone (Malayan Nat. Jour. 23: 31, 32. *1 fig.* 1969). This new station considerably lessens the gap in the previously cited distribution, between Thailand and Sumatra.

Malay Peninsula. PAHANG. Cameron Highlands near Brinchang Village, *Stone 5700* ☿ (A).

SUPPLEMENT TO THE INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species in the following list: 1. *Zanthoxylum scandens*; 2. *Zanthoxylum nitidum*; 5. *Zanthoxylum avicennae*; 6. *Zanthoxylum megistophyllum*; 7. *Zanthoxylum forbesii*; 9. *Zanthoxylum retroflexum*; 10. *Zanthoxylum rhetsa*; 14. *Zanthoxylum pluviatile*; 15. *Zanthoxylum conspersipunctatum*; 16. *Zanthoxylum integrifoliolum*; 17. *Zanthoxylum ovalifolium*; 18. *Zanthoxylum acanthopodium*.

Backer *5753* (1); *11431* (5); *20669* (10); *22526*, *25365* (1); *27132*, *29457* (10); *32842*, *34281*, *34282* (2)
Bakhuizen *5758* (2)
Becking *49*, *70* (10)
Beer's Collectors *BSIP 7376* (6)
Beumée *1930* (10)
Borssum Waalkes *324*, *563* (10)
Bruggeman *448* (1)
Carr *11583* (14); *11952*, *11953*, *14730* (17)
Chang *3136* (16)
Chew & Corner *RSNB 4895* (5)
Craven & Schodde *107*, *260* (6)
Daoen Limauan *NIFS bb 568* (17)
Docters van Leeuwen-Reynvaan *1003* (2)
Evans *55* (14)
Flenley *ANU 2329* (15)
Hallier *361* (1); *361a* (2)
Henty & Frodin *NGF 27243* (14)
Hildebrand *E 397* (1); *NIFS Ja 4676* (17)
Jensen *8* (5)
Kjellberg *1345* (2)
Koorders *6982* (10); *6983* (7); *6984*, *6985*, *6986*, *6987*, *6988*, *6989*, *6990*, *6991*, *6992*, *6993*, *6994*, *6996*, *7036*, *7038*, *11583*, *11584*, *11585*, *11586*, *13123*, *13683*, *18774*, *20321*, *23481*, *25575* (10); *25993*, *26257* (1); *27521*, *30116* (10); *31553*, *31591* (1); *33408* (2); *33743* (1); *34378* (2); *36500*, *36766* (10); *36908* (2); *42127* (10)
Koorders & Koorders-Schumacher *43376*, *47694* (2)
Kostermans *S 42* (9); *18076* (17); *22042* (7)
Lam *245* (17)
Lörzing *3712* (2); *6221*, *7841*, *9482* (18)
Netherlands Indies Forest Service (NIFS), the following by anonymous collectors: *bb 3* (5); *Ja 2251*, *bb 7223* (10)
Ouwehand *304* (18)
Pesik *NIFS bb 9* (5)
Pigl *246* (1)
Rensh *303* (5); *653* (17)
Royen *NGF 16374* (6)
Sayers & Millar *NGF 19851* (15)
Scheffer *HB 14634* (1)
Schodde *2967* (17)
Schodde & Craven *4110* (6)
Slooten *279* (1)
Smith, J. J., & Rant *253* (1)
Snyder *BSIP 4477* (14)
Steenis *4214*, *4917*, *5181*, *6861*, *12261* (1)
Stone *5700* (18)
Teysmann *HB 14625* (10)
Thorenaar *336* (10)
Winckel *2* (2)
Wirawan *417* (10)
Womersley *NGF 19198* (14); *NGF 24944* (15)
Zwickey *1092* (16)

ARNOLD ARBORETUM
HARVARD UNIVERSITY

NOTES ON THE GENUS GALIPEA (RUTACEAE) IN CENTRAL AMERICA [1]

THOMAS S. ELIAS

IN THE SMALL GENUS *Galipea*, consisting of eight to ten species with a center of distribution in northern South America, are two species which reach eastern Panama. Aublet (1775) first described *Galipea* with a single species, *G. trifoliata*, from French Guiana. Additional species of *Galipea* were soon described, mainly from Brazil. In 1912, Pittier collected a single fruiting collection of *G. jasminiflora* (St. Hil.) Engler in eastern Panama (Darien). This locality represents a disjunction from southern Brazil and Guyana. The second species, *G. panamensis*, described here for the first time, is endemic to Panama, although it is expected to occur in bordering areas of Colombia. Two other species described from Central America, *G. guatemalensis* Standl. & Steyerm. and *G. nicaraguensis* Standl. & Williams do not belong in *Galipea*, but should properly be placed in *Angostura* (*Cusparia*). Nomenclatural problems associated with the valid generic name for *Cusparia* have been treated by Elias (1970), and the taxonomy of the Central American species of *Angostura* will be the subject of a subsequent note.

The genus *Galipea* belongs to the tribe Cusparieae, which comprises approximately 22 to 24 genera confined mainly to tropical South America. The tribe is characterized by palmately compound 1–5-foliolate leaves, rarely simple; flowers regular to zygomorphic; corolla often fused and tubular; stamens usually 5, staminodia often present; carpels 4 to 5, ovules 2, collateral with one slightly superposed on the other; embryo curved to uncinate with little or no albumen, radicle retracted between the cotyledons.

The relationships between the two closely related genera *Angostura* and *Galipea* have often been obscured by the indiscriminate practice of describing new species when generic limits are not clearly understood. The taxonomy of the two genera as well as of most of the tribe Cusparieae is poorly known, due largely to the paucity of collections. Engler (1874) helped to clarify the limits of these two genera by transferring eight species, those with individual mericarps rather than capsules, from *Galipea* to *Cusparia* (= *Angostura*). He observed that the gynoecium in species of *Angostura* was composed of five closely packed but free carpels. In species of *Galipea*, however, the five carpels have undergone partial fusion and form a 5-lobed ovary. Consequently, in fruiting condition the individual

[1] I am grateful to Dr. Robert L. Dressler for providing adequate material of the new species, including preserved flowers for dissection. Dr. Thomas G. Hartley has kindly read the manuscript and offered several useful comments. Dr. Lily M. Perry has graciously proofread and corrected the Latin description.

carpels of *Angostura* develop into separate mericarps, while in *Galipea* a 5-parted capsule is formed. Although the structure of the fruit, apocarpous *versus* syncarpous, has been very useful in distinguishing the two genera, it may not prove to be absolutely reliable. Examples of rutaceous genera which may have capsular as well as apocarpous or at least subapocarpous fruits include *Esenbeckia*, *Evodia*, *Boninia*, *Melicope*, *Tetractomia*, *Pelea*, and *Myrtopsis* (Hartley, 1969).

Additional characters that can be used to separate the two genera may be found in the flowers. In *Galipea* the petals are united into a distinct, often curved tube, while in *Angostura* the petals are free or fused only at the base. The stamens of *Galipea* are inserted near the apex of the corolla tube as opposed to stamens inserted at the base of the disc in *Angostura*. Also the anthers of *Galipea* usually have a small basal appendage while those of *Angostura* lack an appendage. In an attempt to find other characters which would be useful at the generic level, pollen of the two genera was examined and found to be of value. Although material was not available for all species the grains of the species of *Galipea* sampled were large, suboblate to subspherical, coarsely reticulate, and 4–5-porate. In contrast are the medium large, prolate, reticulate, and 3-colporate pollen grains found in species of *Angostura*.

Key to the Central American Species of Galipea

a. Leaves unifoliolate; corolla tube stout, 1.1–1.4 cm. long, the lobes narrowly obovate, acute at the apex, 1.3–1.6 cm. long. ..... *G. panamensis*.
a. Leaves trifoliolate; corolla tube slender, 9–11 mm. long, the lobes oblong to narrowly obovate, obtuse at the apex, 4–5 mm. long. ..... *G. jasminiflora*.

Galipea panamensis Elias, sp. nov.

A *Galipea simplicifolia* (Nees & Mart.) Engler inflorescentiis paniculatis, 0.5–2 cm. longis, corolla tubulosa gracilis, lobis 5 mm. longis differt.

Arbores usque ca. 7 m. altae; rami teretes, leviter sulcati, murini vel bruneoli, glabri, lenticellati, lenticellae ± elevatae. Folia 1-foliolata, petiolata, petioli superne ± alati, expansi et indurati ad basin, articulati prope basin laminae, 9–16 mm. longi; lamina coriacea, elliptica vel anguste elliptica, basi attenuata, apice acuminata, pellucido-punctata, glabra, 11–21 cm. longa, 3–9.2 cm. lata, nervis lateralibus utroque 5–11-jugis subtus prominentibus. Inflorescentiae terminales et axillares; corymbi congesti, ca. 12–22-flori; pedunculi erecti vel semi-erecti, conspicue lenticellati, validi, 1.2–3.5 cm. longi. Flores albi; calyx campanulatus, pellucido-punctatus, puberulus, 3–4 mm. longus, lobis transverse ovatibus, apice acutis minute ciliatis, 0.5–1 mm. longis; corolla puberula, conspicue pellucido-punctata, 2.3–3 cm. longa, tubo cylindrico, arcuato in alabastro, 1.1–1.4 cm. longo, lobis in aestivatione imbricatis, anguste obovatis, apice acutis, dilatatis vel leviter recurvatis, 1.3–1.6 cm. longis, ad 3.5 mm. latis; stamina 6–7, inclusa, apicem tubi versus inserta, filamenta brevissima, haud 1 mm. longa, antherae fertiles binae, basifixae, longitudinaliter dehiscentae,

FIGURE 1. *Galipea panamensis*: a, branchlet with inflorescence, × ½, b, inflorescence, × 1½; c. mature bud showing superposed ovules, longitudinal section, × 3; d, cross section of ovary, greatly enlarged; e, mature capsule at beginning of dehiscence, × 1½; f, endocarp with seed, × 2½. a–f from *Dressler 3682* (holotype A).

4–6 mm. longae; staminodia libera, complanata, 6–8 mm. longa; stylus cylindricus, 10–12 mm. longus, stigmata 5, oblonga, 1–2 mm. longa; ovarium 5-carpellatum; loculi biovulati, ovulis plus minusve superimpositis, placentatio axilis. Capsulae 5-loculares, subglobosae, 1–1.5 cm. longae,

cocci basi apiceque connati, ventraliter ac dorsaliter carinati, dehiscentes a basi fere usque ad medium; endocarpium cartilagineum bivalvatum, 1-spermum, basi integrum, alae apice obtusae; semen ± orbiculatum vel obovoideum, lateraliter parum compressum, pubescens.

Panama. COLON: Santa Rita ridge lumber road, East of Colon, *Correa & Dressler 766* [fls., frts.] (MO), *Dressler 3659* [fls., frts.] (A, MO). PANAMA: Cerro Jefe, in coffee plantation, ca. 700 m. altitude, *Dressler 3682* [fls., frts.] (holotype A, isotype MO).

While most species of *Galipea* have trifoliolate leaves, *G. panamensis* differs in having them unifoliolate. Also, its corymbose inflorescence readily distinguishes this new species from all others in the genus in which the inflorescence is narrowly paniculate. Both *G. panamensis* and *G. jasminiflora*, known only from eastern Panama, presently represent the northernmost occurrence of the genus.

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COVER: The Golden Larch, *Pseudolarix* Gordon

With volume 51 the *Journal of the Arnold Arboretum* begins its second half century of continuous publication. To celebrate the occasion we are pleased to present a new cover format. The cover design is the work of Norman Comeau of the Art Department, Thomas Todd Company, Printers, Boston. We hope from time to time to have drawings of other plants on the cover. The Table of Contents will appear on the back cover. *Eds.*

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THE GENERA OF MOLLUGINACEAE AND AIZOACEAE IN THE SOUTHEASTERN UNITED STATES [1]

A. LINN BOGLE

MOLLUGINACEAE Hutchinson, Fam. Fl. Pl. 1: 128. 1926, nom. cons.

(CARPET-WEED FAMILY)

Scarcely or non-succulent, annual [or perennial], glabrous or stellately pubescent herbs [subshrubs, or shrubs], with mostly prostrate to erect, often much-branched stems from a short, narrow taproot. Leaves simple, narrow to broad, glabrous or pubescent, alternate, opposite, or falsely whorled, exstipulate [or stipulate]. Inflorescence basically cymose, axillary or terminal, diffuse or congested. Flowers sessile or pedicellate, regular, perfect [or imperfect]. Perianth uniseriate, inconspicuous. Sepals (tepals) usually 5 [4], free [or slightly united basally], imbricate or quincuncial, persistent. Petals absent [or small, staminodial in origin]. Stamens 3–10[–20], alternating with the carpels when 3 or with the sepals when 5, hypogynous [or perigynous]; anthers 2-loculate, dehiscing by longitudinal slits; filaments free, united basally [or fascicled when stamens numerous]; pollen 3-colpate, or 3–5-zonicolporoidate. Gynoecium of 3–5

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued through those in volumes 40–50 (1959–1969). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References which the author has not seen are marked by an asterisk.

I wish to thank Dr. Jack Fisher for living specimens of *Sesuvium Portulacastrum*, and Dr. John Thieret for specimens of *Trianthema Portulacastrum*. Thanks are also due to Miss Rachel A. Wheeler, who drew the illustrations of *Mollugo*, to Miss Virginia Savage, who drew the remaining illustrations, and to Mrs. Nancy Dunkly, who checked the bibliography and typed the manuscript.

I am particularly grateful to Dr. Wood for his help during the course of this work, and for his careful editing of the manuscript. Dr. John Thieret very kindly read the manuscript and made several helpful comments.

free or united carpels, when united the ovary superior, 3–5-loculate; styles or sessile stigmas as many as the carpels; ovules one per carpel and basal, or several to many on axile placentae, anatropous to anacampylotropous. Fruit an achene or 3–5-valved loculicidal capsule. Seeds reniform to roundish; seed-coat smooth, punctate, tuberculate, or longitudinally ridged; saccate caruncle or hilar peg present or absent. Embryo peripheral, curved; cotyledons fleshy; endosperm starchy. TYPE GENUS: *Mollugo* L.

A small family of 14 more or less weedy genera containing about 95 species distributed primarily in the tropics and subtropics of both hemispheres. The family is best developed in southern Africa, where twelve genera occur. Of these, seven are confined to Africa (*Adenogramma* Reichenb., *Coelanthum* E. Mey. ex Fenzl, *Hypertelis* E. Mey. ex Fenzl, *Pharnaceum* L., *Polpoda* Presl, *Psammotropha* Eckl. & Zeyh., *Suessenguthiella* Friedr.), three extend to southwestern Asia (*Corbichonia* Scop., *Limeum* L.) or southeastern Asia (*Gisekia* L.), and two are pantropical weeds (*Glinus* L., *Mollugo* L.). *Glischrothamnus* Pilg. is known only from Brazil, and *Macarthuria* Hueg. is restricted to Australia. *Mollugo* and *Gisekia* are each represented in our area by a single species, *Glinus* by two. *Gisekia* has only recently been found in Florida, and is thus not included in the older floristic works.

The genera included here have appeared in the literature under several family names. Bentham & Hooker considered them a tribe, Mollugineae, in their order Ficoideae (family Ficoidaceae). Baillon recognized a series Mollugineae in his family Portulacaceae. In the two editions of Engler & Prantl's *Die Natürlichen Pflanzenfamilien* they appear in the Aizoaceae, and in both Small's *Manual of the Southeastern Flora* and the *North American Flora* under Tetragoniaceae (= Aizoaceae). However, taxonomic opinion (Hutchinson, 1926, 1959; Friedrich, 1955; Takhtajan, 1959; Adamson, 1960; Eckardt, 1964; Cronquist, 1968) is now heavily in favor of segregating this group from the Aizoaceae. In this case the family name Molluginaceae Hutchinson is conserved against Glinaceae Link.

Of the four tribes now recognized in the family (Eckardt), only the Mollugineae (including *Mollugo* L., and *Glinus* L., with carpels united and several to many seeds per locule) and Gisekieae (containing only *Gisekia*, with apocarpous gynoecium and solitary, basal ovules) reach our area, while the tribes Corbichonieae (formerly Orygieae) and Limeeae are confined to the Old World.

From the related Aizoaceae the Molluginaceae differ in having a scarcely (if at all) succulent habit; in possessing red pigments of the anthocyanin rather than the betacyanin type; in lacking anomalous secondary growth in the stems and roots; in having floral parts few, usually free (except in *Coelanthium*), hypogynous, and cyclically arranged; and in lacking a calyx tube. The family is considered to be closely allied with the Phytolaccaceae through the apocarpous gynoecium of *Gisekia* and the solitary,

basal ovules of the tribe Limeeae, but differs in having cymose-dichasial, rather than racemose or spicate, inflorescences. There are also relationships with the Portulacaceae and Caryophyllaceae.

Available chromosome counts indicate that $x = 9$ for the Molluginaceae, with several levels of polyploidy represented in the common genera and species.

From a study of the floral morphology and vascular anatomy of seven species in four genera (*Gisekia*, *Glinus*, *Mollugo*, *Semonvillea* [*Limeum*]) Sharma (1963a) concluded that progressive condensation of the floral axis has resulted in a change from acyclic to cyclic origin of the tepals and tepal traces and from independent origin of the tepal and stamen traces to various stages of cohesion and adnation. In the androecium he suggests reduction from three pentamerous cycles to one (the innermost); in the gynoecium reduction from three bundles in each carpel to two in *Limeum pterocarpum* (Gay) Heimerl (as *Semonvillea pterocarpa* Gay) through the loss of the dorsal bundle; and in the placentation reduction from axile to basal (*Gisekia*) or partially parietal.

The embryology of a few genera (*Gisekia*, *Glinus*, *Limeum*, *Mollugo*, and *Corbichonia*) has been studied, although not intensively. Ovules vary from anatropous to anacampylotropous. The inner of two integuments forms the micropyle. An aril may be present around the funiculus (*Glinus*, *Corbichonia*, *Macarthuria*). A normal Polygonum-type embryo sac develops within the crassinucellar ovule, followed by either a caryophyllad or solanad type of embryogeny. Anthers are tetrasporangiate. The pollen grains are 3–5-colpate or zonicolporoidate (i.e., distributed around the equator of the grain; Sharma) and are usually 3-celled when shed.

The family is of no great significance either economically or horticulturally, but individual species may be utilized regionally as vegetables or in folk medicine or serve as grazing plants for livestock.

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KEY TO THE GENERA OF MOLLUGINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *low herbs with simple, alternate, opposite or falsely whorled, often distinctly unequal, exstipulate leaves; stems mostly prostrate*

(to ascending); inflorescence an axillary or terminal, diffuse or congested cyme; flowers incomplete, small and inconspicuous, regular, hypogynous; sepals 5; petals none; stamens mostly 3–5, alternate with the sepals (or with the carpels when 3), free or slightly united basally in a shallow ring; carpels 3–5, free or united in a several-loculate superior ovary; ovules 1 to many; placentation basal or axile; fruit an achene or many-seeded loculicidal capsule; seeds ± reniform, the seed-coat smooth, punctate, tuberculate, or longitudinally ridged.

A. Plants glabrous; seeds lacking caruncle and filiform appendage.
   B. Carpels 5, free; ovule 1, basal; fruit a thin-walled achene; petiole margins often decurrent on the stem, the ribs often bearing scale-like hairs. ..... 1. *Gisekia.*
   B. Carpels 3(–5), united; ovary 3(–5)-loculate; ovules numerous in each locule on axile placentae; fruit a 3(–5)-valved loculicidal capsule; petiole margins not decurrent. ..... 2. *Mollugo.*

A. Plants thinly to densely stellate-pubescent; seeds numerous, each bearing a long filiform appendage and a whitish, saccate caruncle around the persistent funiculus; sepals mucronate tipped; ovary compound, 3(–5)-loculate; stigmas 3(–5), sessile or nearly so. ..... 3. *Glinus.*

Tribe GISEKIEAE Endl.

1. **Gisekia** Linnaeus, Mant. Pl. Alt. 554, 562. 1771.

Scarcely succulent annual herbs with prostrate to ascending branches radiating from a central axis. Stems glabrous, reddish, subequal, with opposite branching; nodes swollen. Leaves exstipulate, opposite to fasciculate, the fascicles separated by distinct internodes; blades narrowly lanceolate to linear-oblong, unequal, entire, the margins sometimes revolute at maturity; midvein prominent below, depressed above, secondary veins inconspicuous; margins of the petiole or leaf-base decurrent, forming ribs on the terete stems. Inflorescence an axillary or terminal several-flowered compound dichasium [varying to umbellate]. Flowers small, perfect [or imperfect], about 2 mm. long. Sepals 5, free, boat-shaped, translucent margins whitish below, pinkish above. Stamens 5[–15], alternate with the sepals; filaments basally dilated; anther basifixed, 2-loculate at anthesis, dehiscing by lateral longitudinal slits, white. Gynoecium apocarpous, carpels 5 [3 or 10], laterally compressed, wall translucent, covered with soft, whitish papillae, at maturity the carpel margins weakly erose-winged; style short, inserted on inner side of summit of carpel, erect in bud, curving outward at maturity; stigma ± terminal; ovule solitary in each carpel, basal. Fruit a thin-walled achene. Seed nearly circular in outline, laterally compressed ± lenticular in section; seed coat black, lustrous, finely punctate at maturity. Embryo nearly annular, peripheral; cotyledons oblong, fleshy; endosperm starchy. TYPE SPECIES: *G. pharnacioides* L. (Named for Paul Dietrich Giseke, 1741–1796, professor at Hamburg, Germany.)

A small genus of perhaps five species distributed primarily in the warmer, drier parts of tropical and subtropical Africa and Asia. The most

widespread of these, *G. pharnacioides*, $2n = 36$, is the only species occurring in our area, apparently as a very recent adventive. Godfrey described and illustrated plants of this species from orange groves in Orange and Polk counties in central peninsular Florida, where they flourish, sometimes in large numbers, in loose cultivated sands. The species may be spreading from this area. This habitat is similar to that of the Indian representatives of this species (which the plants of our area closely approach) as described in detail by Joshi & Kambhoj, who rarely found the species in other than sandy habitats, with the plants appearing after the first few rain showers and the life-cycle being completed in five to eight weeks. This species, with its leaves with large, thick-walled epidermal cells bearing thick cuticle and wax layers and the palisade cell layers internal, is well adapted to xerophytic conditions. The stems, leaves, and all floral organs are conspicuously white-flecked by bundles of raphides produced in the parenchymatous tissues.

There is disagreement concerning the systematic position of the genus. It has been referred to the Phytolaccaceae (DeCandolle, Baillon, Heimerl) but was excluded from that family by Walter; to the Portulacaceae (Gagnepain), a position that has found no support from other workers; to the Ficoidaceae or Aizoaceae (Bentham & Hooker, Pax & Hoffmann); and, most recently, to the Molluginaceae (Hutchinson, Friedrich, Eckardt, Takhtajan, Cronquist). In the Aizoaceae, Molluginaceae, and Phytolaccaceae *Gisekia* comprises a monotypic tribe, Gisekieae Endl. With the Phytolaccaceae *Gisekia* shares free carpels with solitary, basal ovules. Among the genera of Molluginaceae *Gisekia* is perhaps closest (but only distantly related) to *Limeum*. In its anacampylotropous ovules with few-layered nucellar epidermal caps *Gisekia* compares favorably with other Molluginaceae, rather than Phytolaccaceae. It differs from those species of Aizoaceae so far investigated in lacking radially stretched epidermal cells in the nucellar caps and in the absence of starch grains in the embryo sac. The pollen is tricolpate and three nucleate when shed (Sharma, 1963b; Joshi & Rao). Secondary growth is normal, rather than anomalous. The floral vascular anatomy of *G. pharnacioides* has been described by Sharma (1963a). The nature of the red pigments, whether antho- or betacyanous, has not yet been determined.

Orthographic variations of the generic name include *Giesekia*, *Gieseckia*, *Giseckia*, *Gisechia*, and *Giesechia*, while the specific name may appear as "*pharnaceoides*", rather than as the original "*pharnacioides*" (Adamson).

The genus is of little economic significance. *Gisekia pharnacioides* is an important grazing plant for cows, goats, sheep, and camels in India, and is used in folk or Ayurvedic medicine against a broad range of complaints, including scabies, rhinitis, bronchitis, leprosy, leucoderma, urinary diseases, and as a powerful antihelminthic in cases of *Taenia* (tapeworm) infection. The leaves are used in the preparation of *dal* (the split seeds of various legumes), and as a potherb in times of famine (Uphof).

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Tribe MOLLUGINEAE [Fenzl]

2. **Mollugo** Linnaeus, Sp. Pl. **1**: 89. 1753; Gen. Pl. ed. 5. 39. 1754.

Rather variable glabrous annual herbs [or subshrubs] of dry, open, disturbed habitats. Stems prostrate to decumbent, radiating from a short, slender, tapering taproot, dichotomously much-branched, slender, wiry, with slightly swollen nodes. Leaves simple, unequal, exstipulate [or stipules rare, obsolete or early deciduous], scarcely fleshy, forming basal and cauline whorls of 3–8, the whorls often separated by long internodes, basal leaves usually largest, up to 4 cm. long, cauline leaves gradually reduced upwards; blades linear lanceolate to oblong, elliptic, spatulate or obovate, the apex acute to obtuse, the base gradually tapering to a short, membranaceous-margined petiole. Inflorescence an axillary [or terminal] umbellate cluster of 2–5 inconspicuous, short-pedicellate flowers, the pedicels strongly reflexed after flowering. Sepals 5, free, imbricate (or quincuncial), green without, whitish within, margins hyaline, spreading at anthesis. Petals none.[2] Stamens usually 3 and alternate with the carpels, sometimes 4 or 5 [rarely more] and alternate with the sepals, united basally by a very shallow ring of filament tissue; anthers versatile, the 2 lobes separated below. Carpels 3[–8], syncarpous; styles 3[–5], free, very short, erect, recurved; stigma linear, papillate; ovary superior, 3-loculate; ovules numerous in each locule, the placentation axile. Fruit a thin-walled 3[–5]-loculate, ellipsoidal capsule, longer than and included within the persistent sepals, dehiscing loculicidally by 3[–5] persistent valves, the partitions separating from the persistent central axis bearing the funiculi of the ovules. Seeds numerous, somewhat compressed, reni-

[2] I could find no evidence in the many North American specimens of *Mollugo verticillata* in the Harvard University Herbaria (A, GH, NEBC) of the five white, petaloid staminodia described for this species by Ahles (in Radford, Ahles, & Bell, 1968).

FIGURE 1. MOLLUGINACEAE. a–h, **Mollugo.** *M. verticillata*: a, part of a flowering plant, from above × ½; b, flowering and fruiting branch enlarged, × 4; c, flower, × 15; d, flower with forward sepals depressed to show enlarging superior ovary and hypogynous stamens, × 15; e, cross section of ovary showing placentation, × 15; f, mature fruit before dehiscence, with persistent sepals and stamens, × 8; g, fruit after dehiscence, × 8; h, seed with peglike hilum, × 25. i, **Glinus.** *G. lotoides*: seed — note long coiled appendage and inflated aril around funiculus, × 25.

form to roundish, reddish- to blackish-brown; seed-coat bearing 3–7 prominent to obscure longitudinal ridges or smooth; a distinct hilar peg present, but caruncle and filiform appendage lacking. Embryo peripheral, curved around a small amount of hard, semi-transparent endosperm; cotyledons oblong, fleshy. LECTOTYPE SPECIES: *M. verticillata* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 35. 1913. (An ancient generic name derived from Latin "*Mollitie plantae*", pliant or delicate

plants; see Linnaeus, Crit. Bot. 109. 1737; Philos. Bot. 157. 1751).— Carpet-weed, Indian chick-weed, Devil's grip.

A genus of about 35 species native to the tropics and subtropics of both hemispheres, but now widespread in temperate regions in North America and Europe as a weed of disturbed areas. Wilson lists nine species in the *North American Flora*, but these are mainly distributed in the West Indies and Central and South America. Only *Mollugo verticillata* L., $2n = 64$, occurs in our area, ranging from Florida northward through New England to Nova Scotia, westward to Ontario and North Dakota, southward to Texas, New Mexico, and Mexico, while on the Pacific coast it ranges from southern California northward to Oregon, Washington, and Idaho. A second species, *M. Cerviana* (L.) Seringe, $2n = 18$, ranging from Arizona to Lower California and Mexico, is distinguished from the relatively large, coarse, mat forming plants of *M. verticillata* by its small, ascending, diffuse habit, filiform stems, small linear leaves, long-pedicellate flowers usually with five stamens, and seeds with a reticulate seed-coat. This species has been reported to occur on ballast in the vicinity of New York City.

In our area *Mollugo verticillata* may occur in almost any disturbed situation, including cultivated ground, roadsides, railroad beds, sandy river banks, exposed lake-bottom muds, beaches, sand-dunes, and gardens. It flowers from spring to fall. Similar open or disturbed habitats are reported in autecological studies in India by Bakshi & Kapil on *M. Cerviana*, *M. nudicaulis* Lam., $2n = 54$, and "*M. hirta* Thunb." (= *Glinus lotoides* L.). The species are adapted to xerophytic conditions, with short life cycles that progress from germination after a few seasonal showers to flowering and fruiting within a few days, to death within 30 to 45 days. Self and insect pollination and wind dispersal of seeds are reported for these species.

The genera *Coelanthum*, *Glinus*, *Hypertelis*, and *Pharnaceum* are closely allied to *Mollugo*, which is possibly the most primitive of the group, being least specialized in habitat, habit, and floral structure (Adamson). The species of *Glinus* were treated by Bentham & Hooker and in parts of *Index Kewensis* as synonyms of *Mollugo*, an unfortunate taxonomic judgment that created much nomenclatural confusion in the literature.

Scattered chromosome counts for seven species of *Mollugo* indicate a polyploid series with diploid numbers of 18, 36, 54, and 64.

The genus has attracted relatively little interest. Howell described a complex of endemic evolution among eight closely related species in the Galapagos Islands in which two divergent lines have developed from a single variable glabrous annual prototype that had flowers with three or five stamens, a condition found in *M. verticillata*, to which the Galapagean species are "perhaps most closely related." Differentiation has resulted in "one line developing a subshrubby perennial habit and large flowers, the other line developing a low woody caudex and strikingly

glandular herbage. In both lines there is an increase in the number of stamens, approaching or equalling eight, the sum of the five stamens opposite the sepals and the three stamens alternate with the cells of the capsule, two staminal arrangements which occur in the *M. verticillata* type. The geographic separation of the several forms on the different islands has undoubtedly been an important factor in the segregation and maintenance of the specialized developments."

Payne described several interesting anatomical features exhibited by *Mollugo verticillata*, including an increase in thickness of the cortical tissues to produce swollen nodes, pseudoannulation in the xylem of the stems and roots, and the presence of rosettes of cells in the leaf epidermis representing vestigial trichome bases. Anomalous secondary thickening, reported by Metcalfe & Chalk (after Solereder) for "*M. radiata* R. & P." (= *Glinus radiata* (Ruiz & Pav.) Rohrb.) pertains to *Glinus* and has not been found in species of *Mollugo*. The floral vascular anatomy of three species of the genus has been described by Sharma. Excellent illustrations of the seeds of *M. verticillata* and *M. Cerviana* are provided by Thieret. Stomata of the ranunculaceous type occur on both surfaces of the leaves, while clustered and single crystals of calcium oxalate are found in tissues of the leaves and stems. Tartaric acid, tannins, and bitter glucosides, but no alkaloids, have been found in *M. nudicaulis*. Pollen grains with four germ pores and a two-celled condition at shedding are recorded for *M. verticillata* (Payne), in contrast to the three-celled condition reported elsewhere in the family, and Sharma reports pollen grains three-colporoidate in *M. nudicaulis*, and three- to five-zonicolporoidate in *M. pentaphylla* L.

Embryological studies by Payne (*Mollugo verticillata*), Bhargava (*M. nudicaulis*), and Kshirsagar (*M. stricta* L.), indicate that ovules are anacampylotropous at fertilization. Embryo-sac development is normal (Polygonum type), while development of the embryo is probably of the solanad type. Endosperm formation is initially free-nuclear, later becoming cellular.

The genus is of no economic importance. Plants of *Mollugo Cerviana* and *M. pentaphylla* are used in the Old World as a vegetable and in folk medicine against a wide variety of complaints, including skin disorders and diarrhoea, or as a mild laxative.

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3. **Glinus** Linnaeus, Sp. Pl. **1**: 463. 1753; Gen. Pl. ed. 5. 208. 1754.

Annual herbs, with radiating, much-branched, procumbent to ascending stems, forming mats up to 0.5 m. in diameter. Foliage and axes covered with a dense, short, whitish, stellate pubescence, particularly when young [or glabrous]. Leaves alternate to whorled, exstipulate, unequal, entire, ± fleshy, elliptic to ovate, spatulate, obovate or orbicular, gradually narrowed below to a slender petiole, apex rounded to abruptly acute. Inflorescence a dense, sessile to short-pedunculate axillary dichasium. Flowers few to numerous, sessile to short pedicellate. Sepals 5, free, externally stellate-tomentose, margins hyaline, tip mucronate, aestivation quincuncial, persistent. Stamens (3–)5[–20], alternate with and shorter than the sepals [or fascicled when numerous], hypogynous; filament filiform, anther versatile, 2-loculate at anthesis, the 2 lobes separated above and below the point of insertion, dehiscence dorsilateral by longitudinal slits. Carpels 3(–5), united; styles wanting; stigmas 3(–5), sessile, of hyaline papillae, persistent [or styles 3–5, short, erect]; ovules numer-

ous, anacampylotropous, the placentation axile. Fruit an ovoid, loculicidal capsule, the 3(–5) valves separating from a central axis bearing the funiculi and sterile ovules. Seeds numerous, reniform, with a short funiculus enclosed within a bladder-like caruncle and a long filiform appendage coiled round the seed; seed-coat tuberculate to nearly or quite smooth and shiny, reddish- to blackish-brown. Embryo curved; cotyledons oblong, fleshy, endosperm starchy. TYPE SPECIES: *G. lotoides* L. (Name from Greek *glinos*, sweet juice, the significance not clear.)

A genus of about thirteen species with pantropical distribution, reaching temperate areas as an introduced weed. Two species are found in our area. *Glinus lotoides* L., with obovate to orbicular leaves and usually tuberculate seeds, has been found from Louisiana (Thieret) to Oklahoma, Arkansas, and Missouri, in moist situations on alluvial muds and sands on the margins of rivers and lakes, as well as on moist forest soils. *Glinus radiatus* (Ruiz & Pav.) Rohrb., with narrower leaves and smooth seeds, is reported from Louisiana, Oklahoma, and California, southward in Mexico to Central America, and in the West Indies. These two species are distinguished primarily on the texture of the seed coat (cf. Wilson), but the limits of their variation and distribution in the southern United States appear rather indefinite, suggesting the need for further collection and study.

Although considered distinct by Linnaeus, *Glinus* was later reduced to synonymy under *Mollugo* L. by Bentham & Hooker and in the earlier volumes of the *Index Kewensis*. The extensive and very confusing synonymy which resulted is discussed in detail by Pitot. *Glinus lotoides* frequently appears under the synonym *Mollugo hirta* Thunb. The genera are now generally accepted as distinct, with *Glinus* differing from *Mollugo* principally in the presence of a conspicuous caruncle and a filiform appendage (frequently mistaken for the funiculus) on the seed, and in the dense stellate pubescence of *Glinus*. Adamson (1960) suggests that *Glinus* was derived from the same stock as *Mollugo*, but along a distinct line, and that the Brazilian *Glischrothamnus* Pilg. is derived from *Glinus*.

Chromosome counts of $2n = 36$ have been reported for both *Glinus lotoides* and *G. oppositifolius* (L.) A. DC. The report by Solereder (repeated in Metcalfe & Chalk) of anomalous secondary thickening in stems and roots of *G. radiatus* (as *Mollugo radiata* Ruiz & Pav.) should perhaps be reconfirmed. Both anomocytic and paracytic stomatal types occur in the leaf epidermis (Inamdar). The floral vascular anatomy of *G. lotoides* and *G. oppositifolius* is described by Sharma. The embryology of only *G. lotoides* is known. The walls of the tetrasporangiate anther are four cell-layers thick. The cells of the single tapetal layer each contain two to three many-nucleolated nuclei. Mature pollen grains are tricolpate (Sharma), and distinctly three-celled when shed. Ovules are anacampylotropous and crassinucellate, with two integuments. The caruncle (or "aril") may finally enclose as much as the lower third of the ovule in some instances, but its size varies in different specimens, and seeds of

G. lotoides lacking the caruncle are illustrated by Pitot. Embryo-sac development is of the Polygonum type, and the mature embryo sac contains abundant starch grains.

The genus is of no commercial value. In India the leaves of *Glinus lotoides* and *G. oppositifolia* are used as a vegetable or as an appetizer. As an herb the plants are used as a purgative or as a remedy for diarrhoea, itches, and skin diseases.

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(Mesembryanthemum Family)

Slightly fleshy to markedly succulent annual or perennial herbs and low subshrubs [or shrubs], with glabrous, papillose, or pubescent, prostrate to erect and usually much-branched stems spreading from a small, narrow taproot, often forming mats. Leaves ± succulent, cauline, alternate or opposite, stipulate or exstipulate, sessile or petiolate, the petioles often dilated, the membranaceous margins sometimes decurrent, or connate in a sheath about the node; blades simple, entire, flattened to ± cylindrical, glabrous, papillate or pubescent. Flowers mostly inconspicuous, regular, perfect; axillary or terminal (but appearing axillary), sessile to pedicel-

late, solitary, paired, or few in a cymose or spike-like cluster [or inflorescence a dichasium], often flanked by a pair of small, sessile, marcescent bracts. Sepals (tepals) (3–)5, equal or unequal, united below in a usually shallow tube, the tube free from or united with the ovary, the lobes imbricate or quincuncial, erect, hooded or incurved above, ± fleshy, sometimes keeled and bearing a subapical dorsal appendage, greenish without, white or pink to purplish within, persistent or falling as a unit. Petals none [or few to numerous, staminodial, often colorful]. Stamens (1–)3, 5, (7–)10(–13), to numerous, solitary or in pairs or groups alternate with and opposite the calyx lobes or in a continuous cycle, free or united basally, inserted on the floral tube, persistent or falling with the sepals; anthers 4-sporangiate, 2-loculate at anthesis; pollen mostly 3-colpate or colporoidate. Carpels rarely 1 or 2, usually 3–5[–20], united; styles as many as the carpels, free or united below; ovary superior or half-inferior [to inferior], 1–5-loculate or incompletely 2-chambered by a horizontal partition; placentation axile, basal, or parietal, ovules 1 to numerous, campylotropous, arillate or exarillate. Fruit a loculicidal or circumscissile capsule or bony and indehiscent, bearing several sharp horns. Seeds 1 to numerous, small, ± reniform to pyriform, smooth to wrinkled or tuberculate-striate, brown to black; embryo ± curved to annular; endosperm starchy, hard and semitransparent or soft and white. TYPE GENUS: *Aizoön* L.

A family of about eleven more or less weedy genera (including *Tetragonia* and *Mesembryanthemum, sensu lato*, but excluding the fourteen genera now segregated in the Molluginaceae) and approximately 2500 species, with a primary center of distribution in South Africa, but also well developed in the Mediterranean region and Australia, and distributed in dry regions of the tropics and subtropics of both hemispheres. Five genera (*Cypselea, Galenia, Sesuvium, Tetragonia, Trianthema*), and six species occur in our area, mainly as strand plants or weeds of waste places.[3]

Only two of the six subfamilies now recognized in the family (Schwantes, Eckardt) reach our area: the monotypic Tetragonioideae Lindl., with apetalous flowers, half-inferior ovaries, and stony indehiscent fruits, and the Aizoöideae, containing ten apetalous genera with superior ovaries and capsular fruits. The subfamilies Aptenioideae, Hymenogynoideae, Caryotophoroideae, and Ruschioideae are either largely or entirely confined to Africa. The family appears to reach an evolutionary climax in the genus *Mesembryanthemum, sensu lato*, with its many curious, strongly succulent plants and striking flowers with many colorful petaloid staminodia. *Mesembryanthemum* has been split into about 120 segregate genera

[3] The monotypic genus *Geocarpon* Mackenzie, disjunctly distributed in southwestern Missouri (Greene, Jasper, Polk, and St. Clair counties) and southeastern Arkansas (Drew and Bradley counties), and cited under Aizoaceae by various authors (Fernald, Gleason, Pax & Hoffmann, Wilson), has been transferred to Caryophyllaceae by Palmer & Steyermark (1950) as the type of a monotypic tribe Geocarpeae (in subfam. Alsinoideae).

and elevated to family rank (see Ihlenfeldt, Schwantes & Straka, 1962; Eckardt, 1964; Pax & Hoffmann, 1934; for literature citations and accounts of the systematics of this difficult group).

In the older, more conservative sense the Aizoaceae consisted of a broad and ill-defined alliance of about 25 genera (including those now placed in Molluginaceae) that has appeared in the literature under several family names, including Aizoaceae (Pax, Pax & Hoffmann), Ficoidaceae (Bentham & Hooker, De Candolle, Jussieu), Sesuviaceae (Horaninow), and Tetragoniaceae (Small, Wilson). The question of the correct family name has been problematical (cf. Sprague, Rowley, Friedrich), but Aizoaceae is now conserved. In the older literature various genera have been attributed to such related families as Caryophyllaceae, Phytolaccaceae, and Portulacaceae, or more recently placed in segregate families such as Molluginaceae Hutchinson, *nom. cons.* (Rohrbach), Mesembryanthemaceae Fenzl, *nom. cons.* (Lindley; Endlicher; Ihlenfeldt, Schwantes, & Straka; Schwantes), or Tetragoniaceae Nakai, *sensu stricto, nom. cons.* Two families, Molluginaceae and Aizoaceae (or Ficoidaceae, including *Mesembryanthemum* and *Tetragonia*), are most often recognized in the recent literature (Cronquist, Eckardt, Adamson, Hutchinson, Friedrich).

The Aizoaceae are distinguished from the Molluginaceae by their characteristically succulent habit, sepals united basally to form a calyx tube, stamens inserted perigynously, and ovary often partly or entirely inferior; by the presence of betacyanin pigments (betalains, reported thus far for 13 genera and 36 species) rather than anthocyanins; and by the frequent occurrence of anomalous secondary growth in stems and roots. The family has long been considered to have been derived from a phytolaccaceous stock, and it is closely related to the Portulacaceae through *Sesuvium* and *Trianthema*. Relationships to the Cactaceae have also been proposed (Buxbaum).

Available chromosome counts indicate a base number of $x = 8$ (or 9) for the "semi-succulent" group (including *Sesuvium*, *Tetragonia*, and *Trianthema*), with diploid numbers of $2n = 16$, 26, 28, 32, 36, 48, and 96; while $x = 9$ for the "succulent" group (largely confined to Africa), with numerous counts of $2n = 18$, 27, 36, 54, 72, and 108 (Darlington & Wylie).

The embryology of the family has not been intensively studied. Available details include tetrasporangiate anthers, with development of the Basic type and containing Ubisch granules (*Sesuvium Portulacastrum*), and pollen grains three colpate (Sharma) and three-celled when shed. Ovules are anacampylotropous to campylotropous and crassinucellar, with the micropyle formed by the inner of two integuments. A third integument or aril, is reported in *Galenia*, *Sesuvium*, and *Trianthema*. Embryosac development is of the Polygonum type (but the Adoxa type has been described for *Mesembryanthemum pseudotruncatellum*). Starch grains are present in the mature embryo sac. Endosperm formation is initially nuclear, becoming cellular (but remaining nuclear up to eleven days after pollination in *Trianthema Portulacastrum*). Embryo development is of

the solanad type, and polyembryony has been reported in *Trianthema Portulacastrum* (Davis).

In a study of the floral vascular anatomy of species of *Galenia*, *Sesuvium*, and *Trianthema*, Sharma (1962) found progressive fusion of the "tepals," and increasing adnation between the perianth tube and the stamen filaments. These trends are accompanied by progressive stelar condensation in the receptacle, resulting in a transition from independent origins of the tepal and stamen traces, to their adnation and origin as common bundles. He concluded that specialization in the androecium among these species has resulted in a reduction from numerous to few stamens, rather than in an increase in number via "dédoublement." In all species the carpel walls were supplied with five or more bundles (as opposed to three in the Molluginaceae), a condition which he considered derived. He considered the "Ficoidaceae" advanced over the Molluginaceae in the possession of fused tepals whose traces arise at the same level from the stele and divide within the receptacular cortex; perigynous stamens; semi-inferior to inferior ovaries whose carpellary traces divide before leaving the cortex; and fewer ovules. The organogeny of the flower in *Tetragonia* and *Trianthema* has been described in detail by Payer.

The family is of economic significance primarily for the many species of *Mesembryanthemum* and related genera cultivated as ornamentals, and for the various species of *Sesuvium*, *Tetragonia*, and *Trianthema* cultivated for use as vegetables or in folk medicine.

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KEY TO THE GENERA OF AIZOACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *fleshy to strongly succulent, glabrous or pubescent, prostrate or erect herbs; stems often much branched and forming mats; leaves cauline, alternate or opposite, simple, entire, flattened or nearly cylindrical, often with dilated petioles, stipulate or exstipulate; flowers small and inconspicuous, axillary, solitary or clustered, ± sessile, regular, perfect; sepals 3–5, united below into a shallow floral tube, the lobes green, white, pink or purplish within; petals none; stamens mostly 3–10 or numerous, solitary, paired, or in groups, alternate with or opposite the sepals; ovary superior or semi-inferior, 1–5 loculate; carpels 1–5, united; ovules and seeds 1–many; placentation axile, basal, or parietal; fruit a loculicidal or circumscissile capsule or bony and indehiscent; seeds reniform to pyriform; seedcoat smooth, wrinkled or tuberculate.*

A. Ovary superior; fruit a loculicidal or circumscissile capsule; leaves alternate or opposite.
  B. Capsule loculicidal by 3–5 valves; ovules and seeds solitary; stamens 8–10, in pairs alternate with the sepals; stems and alternate leaves densely white-pubescent; stipules absent. . . . . 1. *Galenia.*
  B. Capsule circumscissile; ovules and seeds few to numerous; stamens 1 to many; leaves opposite.
    C. Ovary 3–5-loculate; seeds numerous; stamens 5 to many; sepals appendaged, persistent; leaves ± equal; stipules absent. . . . . 2. *Sesuvium.*
    C. Ovary 1- or 2-loculate; leaves unequal; stipules present.
      D. Stamens 5–10; sepals appendaged; ovules and seeds few; cap of the ovary fleshy and crested; stipules scarious. . . . . 3. *Trianthema.*
      D. Stamens 1–3(–5); sepals unappendaged; seeds numerous; cap of the ovary thin-walled and rounded; stipules laciniate. . . . . 4. *Cypselea.*

A. Ovary half-inferior; fruit horned, indehiscent, bony; leaves alternate, exstipulate, the blades flat, ± ovate-triangular, papillose. ..... 5. *Tetragonia*.

Subfamily AIZOÖIDEAE [Schwantes]

1. **Galenia** Linnaeus, Sp. Pl. 1: 359. 1753; Gen. Pl. ed. 5. 169. 1754.

Perennial, much-branched, grayish [or yellowish to green], prostrate [or erect] herbs or subshrubs [or shrubs]; branches woody at the base, forming dense mats, lateral branches alternate, ± secund, spreading; stems and leaves initially densely coarsely villous with loosely appressed, whitish, flattened hairs, becoming ± glabrescent. Leaves alternate [or opposite], secund, entire, fleshy, sessile exstipulate, the epidermis coarsely papillose; leaves variable in size, those of the main stems largest, with blades broadly obovate, tapering below to a broad base, the apex obtuse, younger leaves ± elliptic to obovate and acute. Flowers small and inconspicuous, on short lateral branches, sessile, axillary, solitary or in groups of 2–5 [or inflorescence a terminal, paniculate cyme]. Sepals (4) 5, united below in a shallow floral tube, the lobes erect, the tips curved inward and downward, pubescent without, glabrous and whitish within. Stamens (8–)10, of unequal length, inserted on the floral tube in pairs alternate with and shorter than the calyx lobes; anthers small, yellow; filaments flat, tapering upwards [or filiform]; pollen 3-colpate. Gynoecium of [2–]3–5 united carpels; styles [2–]3–5, free or united below, stigmatic along the inner surface; ovary superior, truncate and [2–]3–5-angled above, the center depressed, 3–5-loculate [or 2- or 1-loculate by abortion]; placentation axile; ovule solitary in each cell, pendulous on an arching funiculus, campylotropous. Fruit a small, leathery, [2–]3–5-angled capsule with depressed apex, dehiscing loculicidally from the top [or indehiscent]. TYPE SPECIES: *G. africana* L. (Named for Claudius Galenus, ca. 130–ca. 200 A.D., noted Greek naturalist and physician of Pergamos in Asia Minor.)

A genus of about 27 species with a natural distribution confined to southern Africa. The genus is represented in our area by one adventive species, *Galenia secunda* (L. f.) Sond. (subg. KOLLERIA), which can be recognized by its prostrate and secund habit, small axillary flowers, paired stamens, superior 5-angled ovary, and one-seeded carpels. The species is represented in the Harvard University Herbaria by only two sheets of a collection by A. H. Curtis (no. *6869*, in 1901) from Pensacola, Florida. In a penned note accompanying one of these Curtis states that "of my Pensacola plants none but #6865 grew on strictly ballast ground, but the seeds of most of them doubtless came in ballast — No. 6869 forms dense mats probably 4 ft. across. Leaves thickish & with cinereous color." These specimens bear flowers but no fruits. Small described the ovary of this species as partly inferior, but in the specimens at hand, and as described by Adamson, the ovary is superior. Seeds from a South African specimen of the species are small, compressed, and semilunate in outline, with a

coriaceous, iridescent blackish-brown seed coat with longitudinal, tuberculate striations. The embryo is curved around a copious starchy endosperm (but is not nearly annular), and has oblong, fleshy cotyledons about as long as the radicle. The continued presence of the genus in our area needs confirmation. A chromosome count for the genus is lacking.

Two subgenera (Fenzl, Sonder, Adamson) or sections (Pax, Pax & Hoffmann) have been consistently recognized in the genus. The composition of the subgenera (GALENIA and KOLLERIA Fenzl) has been emended by Adamson in the only recent treatment of the genus. *Galenia* is closely related to the South African genus *Plinthus* Fenzl, the two forming a group within the tribe Aizoëae (Adamson).

The pubescence in our specimens is simple, but two-armed hairs occur in some species of the genus. Large bladder-like water storage cells are present in the leaf epidermis. In the dried specimens these collapse, giving the leaf surface a pitted appearance. Delicate spiral thickenings of the vessel walls and anomalous secondary thickening are reported for the genus (Metcalfe & Chalk).

The genus is of no economic significance. *Galenia spathulata* Fenzl may be used as fodder for sheep in southern Africa.

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2. **Sesuvium** Linnaeus, Syst. Nat. ed. 10. 1052, 1058, 1371. 1759.

Annual or perennial, prostrate or ascending, succulent, glabrous herbs or subshrubs. Stems several from a short tap-root, sometimes rooting at the nodes, often reddish, branching alternately. Roots fibrous. Leaves opposite, ± equal, entire; blades nearly cylindrical to ± flattened, linear-lanceolate to elliptic or obovate; apex acute or obtuse; petioles dilated, the membranaceous margins clasping [or connate], exstipulate. Flowers perfect, terminal but appearing axillary, solitary or clustered, sessile to long pedicellate, a pair of marcescent bracteoles at the base of the pedicel. Sepals 5, united below, the lobes imbricate, margins scarious, hooded above and bearing a short subapical dorsal mucro, pink to lavender within, spreading at anthesis, persistent. Stamens 5, free and alternisepalous or numerous in groups alternate with the sepals or in a continuous cycle, inserted on the floral tube, shorter than the sepals, persistent; filaments filiform or subulate; anthers small, often reddish; pollen tricolpate [or polymorphous?]. Styles 2–5, linear, erect; stigma longitudinal, papillose;

ovary superior, 2–5 loculate; ovules numerous, anacampylotropous, placentation axile. Capsule membranaceous, enclosed within the persistent perianth, circumscissile near the middle. Seeds numerous, small, roundreniform, smooth, lustrous, black, arillate, the aril membranaceous, tightly investing the seed; embryo annular or slightly coiled; cotyledons oblong, fleshy; endosperm soft, starchy. (Including *Halimum* Loefl., *Halimus* Kuntze, *Squibbia* Raf.) TYPE SPECIES: *S. Portulacastrum* (L.) L. (Name Latin, presumably after *Sesuvium*, land of the Sesuvii, a Gallic tribe, the significance here not explained.) — SEA PURSLANE.

A genus of about eight species distributed in the tropics and subtropics of both hemispheres, inhabiting saline beach-dunes, marshes, hammocks, and disturbed situations in coastal areas. Two rather variable species occur in our area. *Sesuvium maritimum* (Walt.) BSP. (*S. pentandrum* Ell.) with flowers small and sessile or nearly so and five alternisepalous stamens, ranges from Long Island southward to Florida and the West Indies, westward to northern Louisiana and Texas. *Sesuvium Portulacastrum* (*S. sessile* Pers.) $2n = 16, 36, 48$, with larger and distinctly pedicellate flowers and numerous stamens, appears to occur sporadically in the Carolinas, and from Georgia southward through Florida to the West Indies, westward to Texas, and southward to Mexico, Central America, and South America. *Sesuvium crithmoides* Welw., a native of Angola, with long, narrowly linear leaves and sessile flowers, was collected once in 1902 on the waterfront in Brunswick, Georgia, but has not been reported since. In the southwestern United States *Sesuvium verrucosum* Raf., with an often more erect habit, numerous stamens, and vegetative surfaces densely papillate with large epidermal water-storage cells, approaching our area in Oklahoma and Texas, ranges northward and westward through Kansas, Colorado, Utah, Nevada, and central California, and southward to Mexico.

Sesuvium is closely related to *Cypselea* Turp. and *Trianthema* L. It has been recognized as distinct by all authors except Degener & Degener, who reduce it to synonymy under *Trianthema*, stating that the difference between the two genera is mainly "the number of cells in the ovary, a character . . . of trivial importance." These three genera have been consistently allied, and the group is thought to link the Aizoaceae to the Portulacaceae.

Chromosome counts, available only for *Sesuvium Portulacastrum*, indicate the presence of polyploidy and aneuploidy, with base numbers of eight (and nine), and $2n = 16, 32, 36, 48$. The presence of betacyanin has been demonstrated in *S. Portulacastrum*.

Species of *Sesuvium* exhibit structural adaptations to xerophytic conditions. The succulent leaves of *S. Portulacastrum* have stomata on both surfaces and contain subepidermal palisade tissues that are four to five cell-layers thick and enclose a central zone of loose, water-storing parenchyma. In contrast, the leaves of *S. maritimum* contain a homogeneous chlorenchyma interrupted only by large intercellular spaces that underlie

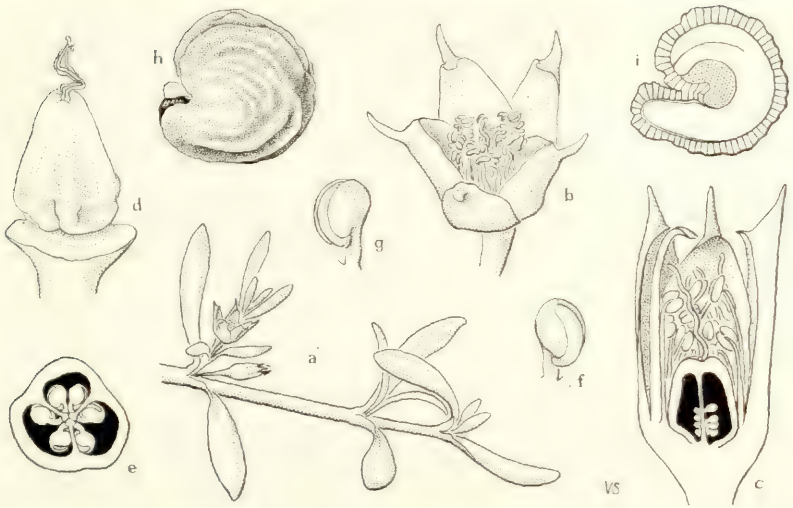

FIGURE 2. **Sesuvium.** a–i, *S. Portulacastrum*: a, flowering branch, × ¾; b, flower, × 3; c, flower in semidiagrammatic vertical section to show slightly perigynous insertion of floral parts, superior ovary, and placentation, × 5; d, mature fruit before dehiscence, perianth removed, × 4; e, cross section of ovary showing three septa and parietal placentation, × 10; f, g, lateral views of ovules at or near anthesis showing aril developing from funiculus, × 25; h, mature seed — note tightly investing membranaceous aril, × 20; i, seed in section, showing curved embryo surrounding endosperm (stippled), diagrammatic, × 20.

large water-storage cells in the epidermis. The epidermal cells have a thickened outer wall with a smooth cuticle. Stomata are of the ranunculaceous type. Crystal clusters occur in cells of the pith, cortex, and leaves. Anomalous secondary thickening is reported in the stems and roots of *S. Portulacastrum*.

The ovules of *Sesuvium Portulacastrum* have two integuments (the inner of which forms the micropyle) and an aril (or third integument). The inner integument is two cell-layers thick, the second integument is initially two layers thick but becomes three layered, while the aril is three cell-layers thick. A Polygonum-type embryo sac is formed, and embryo development probably conforms to the Linum variation of the solanad type. The nucellus immediately above the embryo sac consists of two to three layers of radially elongate cells, while five to six cell-layers are present along the sides of the sac. The endosperm is initially free nuclear, but later becomes cellular. Anthers are tetrasporangiate, with walls five cell-layers thick, the innermost layer forming a glandular, binucleate tapetum. Ubisch bodies are present in the anthers. Pollen grains are three celled when shed.

Sesuvium Portulacastrum is cultivated as a vegetable in some Asian countries.

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3. **Trianthema** Linnaeus, Sp. Pl. 1: 223. 1753; Gen. Pl. ed. 5. 105. 1754.

Succulent, glabrous [or pubescent], herbaceous or suffrutescent, annual or perennial plants of waste places. Stems prostrate or erect, from a short tapering taproot, often much branched, the branches alternate or opposite and usually bearing decurrent lines of hairs from the petiolar sheath to the node below, glabrescent. Leaves opposite, the members of a pair conspicuously unequal; blades glabrous, fleshy, elliptic-lanceolate to spatulate, obovate, or suborbicular, the apex acute or obtuse to truncate-acuminate or retuse, the base acutely tapering to rounded; petiole margins expanded, membranaceous, connate into a sheath around the node, stipulate. Flowers axillary, solitary or cymosely clustered [or inflorescence a dichasium], sessile or short-pedicellate, perfect. Sepals 5, united below and falling as a unit [or persistent], the tube fused with two bracteoles, the petiolar sheath, and even the stem, the lobes imbricate, cucullate, with a sometimes-barbed dorsal mucro just below the apex [or mucro absent], inner surface colored bright- to purplish-pink [or white]. Stamens 5–10, inserted on the floral tube in two cycles alternate and opposite the sepals [or stamens 1–3 or numerous in fascicles alternate with the sepals], shorter than and falling with the sepals; anthers small, rotund

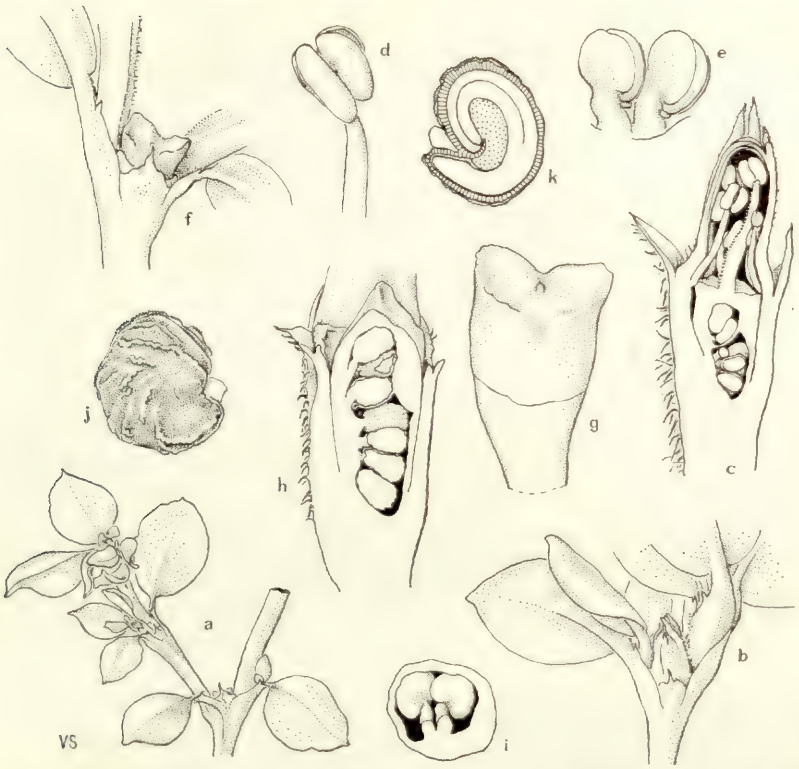

FIGURE 3. **Trianthema.** a–k, *T. Portulacastrum*: a, flowering branch, the axillary flowers hidden by the fused sheathing leaf bases and secondary bracts, × 1; b, an axillary flower with connivent calyx lobes — note sharply pointed secondary bract in foreground between petioles, × 3; c, flower in semidiagrammatic vertical section to show connate sepals, perigynous insertion of floral parts, semi-inferior ovary, parietal placentation, and horizontal septation of locule, × 7; d, stamen, × 20; e, lateral view of two ovules — note aril developing from funiculus, × 30; f, nearly mature fruit inclosed by tube consisting of fused leaf bases, secondary bracts, and perianth — note fleshy cap protruding, × 3; g, same, floral tube removed — note horizontal line of dehiscence between fleshy cap and membranaceous base of pyxis, × 7; h, fruit in semidiagrammatic vertical section, × 5; i, cross section of ovary, showing parietal placentation, × 6; j, seed with tightly investing aril, × 12; k, seed in section, showing curved embryo inclosing endosperm (stippled), × 12.

to oblong; filament filiform; pollen tricolpate. Style 1[–2], short (in ours), excentric; stigma longitudinal, papillate; ovary superior, one or incompletely 2-chambered by a horizontal partition, ± truncate above and bearing an excentric, often bilobed marginal crest [or peripheral corona]; ovules few, campylotropous, arillate, placentation basal or parietal. Capsule superior, ± turbinate, closely surrounded below by the floral tube, walls membranaceous below but fleshy above, apex truncate,

circumscissile near the middle, the fleshy cap exserted and bearing a bilobed marginal crest and including the upper chamber of the ovary. Seeds [1–]several, round-reniform, arillate, wrinkled, reddish-brown to black, the upper 1 or 2 often enclosed in the upper chamber of the ovary and falling with the indehiscent operculum, 2 or more remaining in the lower chamber. Embryo annular to slightly coiled, surrounding the starchy endosperm; cotyledons oblong, fleshy. (Including *Portulacastrum* Juss.). TYPE SPECIES: *T. Portulacastrum* L., $2n = 26$. (Name derived from Greek *treis*, three, and *anthemon*, flower.) — SEA PURSLANE, HORSE PURSLANE.

A small pantropical genus of perhaps 25 species inhabiting sandy seabeaches, hammocks, alkaline or clay soils, and waste places where introduced. The genus has centers of development in Africa and Australia and is represented in our area only by *Trianthema Portulacastrum*, which ranges from New Jersey to Florida and the West Indies, westward to Texas and southern California, northward to Oklahoma and Missouri, and southward to Mexico and Central and South America. The species is quite variable in habit, pubescence, development of the inflorescence, length of the bracteoles and sepals, number and length of stamens, and form of the crest of the operculum.

Two sections were recognized in the genus in De Candolle's *Prodromus* (sect. ZALEYA Burm. f. and sect. ROCAMA Forsk., which included *Trianthema Portulacastrum*). More recently Jeffrey (followed by Adamson) has recognized two subgenera: TRIANTHEMA, with flowers usually solitary and ovaries containing four to numerous ovules, and PAPULARIA (Forsk.) Jeffrey with flowers usually clustered and ovaries containing two superposed ovules. Jeffrey resolved the confused generic limits between *Trianthema* and *Sesuvium* in Africa by reestablishing the genus *Zaleya* Burm. f. to contain the digynous species *T. decandra* L. (locules and stigmas two, operculum two valved). *Trianthema* is also closely related to *Cypselea* Turp.

The few chromosome counts available suggest the development of polyploidy and aneuploidy within the genus, since $2n = 16$ in *Trianthema argentina* Hunziker & Cocucci, *T. decandra*, *T. pentandra* L., and *T. polysperma* Hochst., while $2n = 26$ and 36 in *T. Portulacastrum* (as *T. monogyna*), and $2n = 28$ and 32 in *T. crystallina* Vahl. A relationship between level of ploidy and ecological characteristics in several African species is suggested by Hagerup.

Morphological adaptations to xerophytic conditions are apparent in the leaf structure of *Trianthema Portulacastrum*, in which a central, compact, palisade-like chlorenchyma tissue is bounded above and below by one or two layers of thin-walled water-storage cells and the epidermal layers are uncutinized. Stomata (both anomocytic and paracytic types: Inamdar) occur on both surfaces of the leaf. The upper epidermis consists of large, angular, thin-walled cells, and bladder-like epidermal cells are recorded in *T. crystallina* Vahl. The leaf veins are surrounded by a sheath of

parenchyma cells that lack chloroplasts but contain abundant starch grains. Drusiform clusters of calcium oxalate crystals are abundant in the parenchymatous tissues of the leaf and stem of *T. Portulacastrum*. Anomalous secondary thickening has been reported in *Trianthema*, but its occurrence should perhaps be confirmed.

Embryological studies of *Trianthema argentina*, *T. decandra*, and *T. Portulacastrum* (as *T. monogyna* L.) indicate that ovules are either campylotropous or amphitropous and have a bulky nucellus surrounded by two integuments (the inner of which forms the micropyle) and an aril or "third integument." In *T. argentina* a characteristic air space is reported between the inner and outer integuments at the chalazal end of the ovule, and the cells of the nucellar epidermis are reported to elongate and undergo periclinal divisions to form the nucellar cap (Cocucci), while in *T. Portulacastrum* the epidermal cells are said merely to stretch out radially (Bhargava). Embryo-sac development is of the Polygonum type, and starch grains accumulate in the embryo sac. The endosperm is initially nuclear, but later becomes cellular from the micropylar end. Development of the embryo is of the solanad type (probably the Linum variation). Polyembryony has been reported in *T. Portulacastrum*. The anther walls develop normally and contain five cell-layers at maturity, including a binucleate cellular tapetum. Pollen grains are three celled when shed.

The alkaloid trianthemin (of unknown structure) has been isolated from the Indian drug "punarnava," which is derived from *Trianthema Portulacastrum* (*T. monogyna*) and is used in the Ayurvedic medicine of India in cases of heart disease, anemia, and other disorders. The presence of betacyanin has also been demonstrated in this species.

The genus is of no commercial value, but some species are cultivated as vegetables in eastern Asia. Leaves of *Trianthema Portulacastrum* are used as a vegetable in India and Africa, and a decoction of its roots serves as an emenagogue in the Philippines and may be abortive in large doses. Its root is also used as an amenorrheic or as a cathartic in powdered form with ginger. Ashes of the herbaceous *T. salsoloides* Fenzl are mixed with simson oil and lime in Sudan to make a soap. Plants of *T. pentandra* L. are also used in Sudan as an astringent in abdominal diseases, while the leaves are eaten as a potherb in times of famine, and ashes of the plant are a source of salt for the natives (Uphof). Several species of the genus, including *T. Portulacastrum*, are reputed to be poisonous to livestock because of their content of alkaloids, oxalates, saponins, or nitrates.

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4. **Cypselea** Turpin, Ann. Mus. Hist. Nat. Paris **7**: 219, *pl. 12*, *figs. 0–11*. 1806.

Small, prostrate, glabrous to papillose, fleshy, herbaceous or suffrutescent, densely branched annuals forming small, leafy mats; branches slender, from the top of a short, slender taproot. Branching alternate, sympodial (at least in part). Leaves small, opposite, entire, fleshy, the members of a pair distinctly unequal; blades elliptic to elliptic-oblong or ovate, apex acute or obtuse, base acute to rounded; petiole often as long as the blade, dilated below, the margins scarious, clasping, those of a leaf pair sometimes connate and sheathing the node; stipules scarious, laciniate. Flowers appearing axillary, solitary, small, accompanied in the axil by two small, scarious, laciniate bracteoles. Sepals 5, unequal, erect, united below for about one third their length, the margins scarious, the lobes thicker and slightly keeled above, lacking a dorsal appendage, green or purple-tinged without, white to reddish within, quincuncial, persistent. Stamens 1–5, alternate with and shorter than the calyx lobes, inserted at the sinuses, persistent; anthers small, subglobose, whitish; filaments filiform. Styles 2[–3], very short, erect, slightly united below; ovary

superior, 2[–3]-loculate at anthesis; ovules numerous, campylotropous, exarillate; placentation axile. Fruit a subglobose, 1-loculate, thin-walled pyxis circumscissile below the middle, remnants of the septum remaining; seeds numerous, small, on long funiculi from the persistent central axis, subreniform. Seed coat smooth, brown; embryo arcuate around a scanty, starchy endosperm; cotyledons fleshy. (Including *Radiana* Raf., *Millegrana* Juss. ex Turpin.) TYPE SPECIES: *C. humifusa* Turpin. (Name from Greek, *kypsele*, a hollow vessel or a beehive, probably because of the shape of the pyxis.)

A very small New World genus of possibly three species, inhabiting drying swamp land and other moist, disturbed sites on shore lines, hammocks, and sandy pinelands. The genus is represented in our area by *Cypselea humifusa* in peninsular Florida and in Louisiana; this species is also known from central California. It may have been introduced into all three of these areas from the West Indies (Cuba, Hispaniola, St. Thomas, Guadeloupe, and others).

Cypselea humifusa, usually with green calyx lobes and with stamens mostly one to three, was first described from Haiti (Saint Domingue). *Cypselea rubriflora* Urb., with longer pedicels, reddish calyx lobes and five stamens, has been described from Cuba. *C. Meziana* K. Müll., of Paraguay, is said to differ from both of these species in having three styles and a three-loculate ovary.

The extent and taxonomic significance of color variation in the calyx lobes and other plant parts is not known, since collectors' notes on color are rare. Specimens of a recent collection by Thieret of *Cypselea humifusa* from St. Landry Parish, Louisiana, are lightly tinged with purple in the stems, leaf tips, calyx tube and lobes, and darkly so in the fruits, but such coloration is lost in older herbarium specimens, which become rather brown.

Although plants of the genus are glabrous, the nodes often appear pilose due to the protruding segments of the laciniate bracteoles and stipules. The solitary flowers appear to be axillary but are actually terminal. Growth of the vegetative axis beyond each flower is sympodial, the axillary bud of the larger leaf continuing the axial growth while the axillary bud of the smaller leaf produces only a short fascicle of small leaves. At anthesis the ovary is distinctly septate, with axile placentation, but the septum is ruptured during fruit development, giving the appearance of being unilocular with the free-central placentation that is so often cited in taxonomic accounts. Anomalous secondary thickening and solitary crystals are reported for the genus. Chromosome counts are lacking, and the identity of the red pigments is not known.

The genus is considered to be closely related to *Sesuvium* L. and *Trianthema* L. (Müller).

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Subfamily TETRAGONIOIDEAE Lindl.

5. **Tetragonia** Linnaeus, Sp. Pl. 1: 480. 1753; Gen. Pl. ed. 5. 215. 1754.

Annual or perennial herbs or subshrubs with somewhat succulent, densely papillate [or pubescent], procumbent or ascending, spreading branches. Leaves cauline, mostly alternate, petiolate, exstipulate; blades entire, fleshy, ovate-deltoid to ovate-rhomboid, the apex acute to obtuse, the base mostly truncate to cuneate, papillate [or pubescent]. Flowers axillary [or terminal], solitary or paired [or few in a cymose or spike-like cluster], nearly sessile or short pedicellate, perfect [or polygamous through reduction of the ovary]. Sepals 4 (3–5), fleshy, united in a tube and adnate to the ovary, color varying in ours from greenish to yellowish within [to reddish]. Stamens 7–13 [1 to many, or in fascicles alternate with the calyx lobes], inserted on the floral tube, shorter than the calyx lobes;

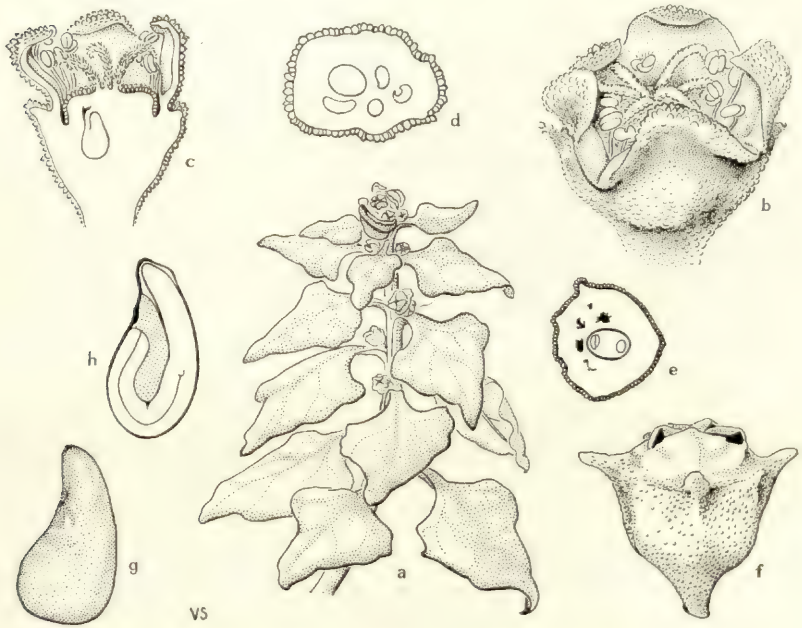

FIGURE 4. **Tetragonia.** a–h, *T. expansa*: a, flowering branch, × ¾; b, flower, × 8; c, flower in semidiagrammatic vertical section to show perigynous floral organs — note solitary pendent ovule in one locule, × 6; d, cross section of ovary showing unequal growth of fertile and sterile carpels, × 8; e, cross section of a fruit – note seed of single fertile carpel, sterile locules crowded out, × 4; f. indehiscent horned fruit, × 3; g, seed, × 10; h, seed in section, to show curved embryo partly inclosing endosperm (stippled), × 12.

anthers subglobose; pollen yellow. Carpels 3–9 [rarely 1 or 2], united; styles 3 or more, equaling the locules, short, erect; ovary half-inferior [to inferior], 3–9-loculate; placentation axile; ovules solitary, pendent, campylotropous (?). Fruit obconic, nutlike, bony, indehiscent, with usually 4 or 5 short, sharp horns [or fruit compound, variously angled to winged or thorny, the thorns often producing axillary buds or sessile flowers in *T. dimorphantha* Pax!]. Seeds solitary, ± pyriform to subreniform; seed coat smooth, membranaceous, light brown; embryo hook or horse-shoe shaped [to arcuate] around an abundant, white, starchy endosperm; cotyledons linear-oblong, fleshy. (Including *Demidovia* Pall.) LECTOTYPE SPECIES: *T. fruticosa* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge, 1930. Nomencl. Prop. Brit. Bot. 159. 1929. (Name from Greek *tetra*, four, and *gonia*, angle, in reference to the fruit; a shortened form of the pre-Linnaean name *Tetragonocarpos*.) — NEW ZEALAND SPINACH.

A genus of about 50–75 species distributed chiefly in the Southern Hemisphere. More than half the species are restricted to southern Africa, while a large number are concentrated in southern South America, particularly in Chile. A few species occur in Australia, New Zealand, Polynesia, southeastern Asia, and North Africa. The genus is represented in our area by *Tetragonia expansa* Murr. (*T. tetragonoides* (Pall.) O. Kuntze), $2n = 32$, of subgenus TETRAGONOIDES. Although native to the coastal regions of the southern and western Pacific, *T. expansa* has been widely cultivated as a leafy vegetable and has become naturalized in many areas after escaping from cultivation. The species is reported from old fields and waste places in North Carolina and Florida, Bermuda, Connecticut and Massachusetts, and California. The number of specimens available is small, however, and it is not clear whether the species is truly naturalized in these areas or occurs only as a waif after escaping cultivation. None of the available specimens is complete; the lower parts are missing from all of them. The broad distribution of *T. expansa* around the shores of the Pacific basin is probably explained by Hashima's finding that the fruits can stay afloat in sea water for more than a month, with the enclosed seeds retaining their viability, thus allowing for long-distance dispersal by ocean currents.

From other genera of Aizoaceae *Tetragonia* is distinguished by its half-inferior to inferior ovaries with a single pendent ovule in each locule, by the absence of staminodial bodies (Adamson), and by its indehiscent, cartilaginous or stony (and sometimes compound) fruits. The genus has been subdivided into two or three sections (Pax & Hoffmann, Post & Kuntze), or two or four subgenera (Fenzl, Adamson). The most recent revision is that of Adamson who recognizes four subgenera: TETRAGONIA (containing seven series), TETRAGONOIDES (DC.) Adamson, ANISOSTIGMA (Schinz) Adamson, and TRIBULOCARPUS (Moore) Adamson. Only subgenus TETRAGONOIDES ranges beyond southern Africa.

The systematic position and relationships of *Tetragonia* are not clear. The genus was once considered close to *Mesembryanthemum* (Baillon,

Bentham & Hooker, De Candolle, Pax) on the basis of floral structure (presence of a floral tube, numerous stamens, half-inferior to inferior ovaries), but more often it has been segregated as the type, if not the sole member, of a tribe Tetragonieae (Fenzl, Müller, Pax & Hoffmann), subfamily Tetragonioideae (Eckardt, Schwantes), or family Tetragoniaceae (Friedrich, Lindley, Nakai).

The chromosome complement of the genus is based on eight, with numbers of $2n = 32$ reported for *Tetragonia expansa*, *T. crystallina* L'Hérit., and *T. echinata* Ait., and $2n = 96$ for *T. trigyna* Banks & Sol. ex Hook. f.

Payer described and illustrated the floral organogeny of *Tetragonia expansa* in detail, but the morphology and anatomy of the genus have received little attention. Secondary thickening in stems and roots is anomalous, producing xylem and phloem in more or less complete concentric rings. Large bladder-like water-storage cells occur in the epidermis among smaller unspecialized cells. In dried specimens these become collapsed and flattened, giving the plant a hoary appearance. Stomata of the ranunculaceous type are reported. Columnar crystals occur in the pith of *T. spicata* L. f., and clustered crystals in the cortex of *T. expansa*.

Apart from a statement of D'Hubert on the presence of starch grains in the embryo sac of the "Tetragoniées" the embryology of the genus is apparently unknown. Coutinho *et al.* investigated the structure of chloroplasts in *T. expansa* and found them intermediate in form between the Euglena and Aspidistra types, in that they contain few, small, irregular grana and a relatively large amount of stroma lamellae extending throughout the length of the chloroplast.

Red pigments of the betacyanin type are reported in *Tetragonia crystallina*. Toxic alkaloids and saponins are also reported for *T. expansa* (as *T. tetragonoides*).

The economic significance of *Tetragonia expansa* appears to rest solely on its cultivation as a leafy vegetable, a substitute for spinach. Analysis of the dried plant, however, has shown that the content of anhydrous oxalic acid may attain levels of 10 per cent or greater, thus posing the danger of sharply reducing the absorption of calcium from a diet containing adequate amounts of that element.

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SEEDLING MORPHOLOGY IN THE JUGLANDACEAE, THE COTYLEDONARY NODE

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DESPITE NUMEROUS STUDIES in the Juglandaceae, the number of genera and their phylogenetic positions are still unsettled. *Alfaroa*, *Annamocarya*, *Carya*, *Engelhardia*, *Juglans*, *Oreomunnea*, *Platycarya* and *Pterocarya* were recognized by Leroy (1955), while Manning (Manning & Hjelmqvist, 1951; Manning, 1961) has continued to emphasize the similarities of *Oreomunnea* (*Engelhardia* sect. OREOMUNNEA sensu Manning) with *Engelhardia* and those of *Annamocarya* (*Carya* sect. RHAMPHOCARYA sensu Manning) with *Carya*, thus arguing for six genera. The walnut family is generally conceded to be a very natural assemblage (Lawrence, 1951; Cronquist, 1968), so it is not surprising that generic boundaries are debatable. This is not to say that the taxa are difficult to characterize; all representatives are, in fact, large forest trees which may be recognized by combinations of features that range from differences in bark and wood (Heimsch & Wetmore, 1939) to phyllotaxy (Standley, 1927), flowers (Manning, 1940, 1948), pollen (Whitehead, 1965), inflorescences (Manning, 1938), and particularly fruits (Leroy, 1955). It is precisely this comparative wealth of information that makes the Juglandaceae so tempting to the phylogenist.

Because of the remarkable diversity of the flowers and fruits and as a result of some preliminary studies on seedling germination, we had reason to believe that seedling morphology would be useful in assessing generic relationships. An earlier study by Davey (1916) on the Amentiferae covered the descriptive aspects of two species of *Carya*, four species of *Juglans*, one of *Pterocarya*, and the monotypic genus *Platycarya*. A wide variety of cotyledonary nodal types is reported in the literature. Trilacunar and multilacunar nodes are noted for *Carya* (Davey, 1916; Langdon, 1934), and *Juglans* (Davey, 1916, 1935; Nast, 1941; Gravis, 1943) and unilacunar two-trace nodes for *Platycarya* and *Pterocarya* (Davey, 1916). This diversity of nodal types, representing both the most primitive and advanced forms as proposed by Marsden and Bailey (1955) in their study of nodal evolution, as well as the absence of information on the primitive members of the family, namely *Alfaroa* and *Engelhardia*, offered additional promise for the current survey. An implicit consideration of our study was an examination of the evidence giving rise to the general belief

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that dicotyledonous seedlings have conservative vascular anatomy (Sinnott, 1918; Foster & Gifford, 1959; Carlquist, 1961; Eames, 1961).

MATERIALS AND METHODS

Of the six genera and 60 species recognized by Manning (1961), 12 species of six genera were sampled (TABLE 1). Seedlings were obtained from field- and greenhouse-grown collections. Field specimens were preserved in formalin-acetic acid-alcohol (FAA) at the same time herbarium specimens were prepared. Most of the seeds were stratified in a standard greenhouse mixture of sand, peat, and loam and stored at 40°F for 85 to 167 days prior to removal to the greenhouse. Fruits of *Engelhardia roxburghiana*, however, were planted in the greenhouse without cold treatment. Seedlings in various stages were killed, fixed, and stored in FAA. Material for sectioning was dehydrated in a tertiary butyl alcohol series and embedded in 61°C Tissuemat. Serial transverse sections of most seedlings were cut at 7 to 12 μ. The older and woodier specimens of *Carya cordiformis* were sectioned at 25 μ on a sliding microtome. Sections were stained in safranin or safranin-fast green. Photomicrographs were taken with a Leitz Ortholux microscope, plano objectives, and Panatomic-X sheet film.

RESULTS

TABLE 1 presents a summary of the cotyledonary nodal survey. This same sequence of species is adopted in the following account of the seedling characteristics.

The monotypic genus *Platycarya strobilacea* Sieb. & Zucc. is a native of eastern Asia and possesses a combination of some of the most primitive and advanced characters in the family (Manning, 1961). The pistillate catkin resembles a spiny cone with the individual bracts remaining attached to the inflorescence at the time of fruit dispersal (Manning, 1940). The minute fruits depend on small lateral outgrowths of the bracteoles for wind dissemination. Seed germination is epigeal. The cotyledons are deeply bilobed and both of the primary lobes are again lobed, but in an unequal fashion (Lubbock, 1892; Hickel, 1914; Davey, 1916; FIGURE 1). The cotyledonary node is unilacunar two-trace (FIGURE 2), with the traces separated by a very narrow band of parenchyma (FIGURE 15). Davey (1916) notes the anatomical similarity of the seedling of this species to that of *Pterocarya*.

The species of *Pterocarya*, a genus with six species and several varieties known from the Caucasus Mountains and eastern Asia (Manning, 1961), have elongate pistillate inflorescences bearing numerous 2-winged fruits that are well adapted to wind dispersal. Germination is epigeal in the three species investigated, including *P. rhoifolia* Sieb. & Zucc. (Davey, 1916), *P. fraxinifolia* (Lam.) Spach (Lubbock, 1892; Hickel, 1914), and *P. stenoptera* C. DC. (FIGURE 3). The thin, foliaceous cotyledons are

TABLE 1. **Survey of cotyledonary nodal anatomy in the Juglandaceae** *

TAXA	COLLECTION DATA	GERMINATION	COTYLEDONARY NODE	
Platycarya strobilacea	Fruit, *Kokawa 9*	epigeal	1-gap	2-trace
Pterocarya stenoptera	Fruit, *Herbst Bros. 5270*	"	1-gap	2-trace
Juglans ailantifolia	Fruit, Gerardi Nursery	hypogeal	3-gap	3-trace
Carya aquatica	Fruit, *Demaree 57353*	"	6-gap	6-trace
Carya cordiformis	Fruit, *Stone 1848*	"	4-gap	4-trace
Carya laciniosa	Fruit, Gerardi Nursery	"	5–6-gap	5–6-trace
Carya ovata	Fruit, *Demaree 57494*	"	3-gap	3-trace
Carya tomentosa	Fruit, *Demaree 55007*	"	3-gap	3-trace
Engelhardia roxburghiana	Fruit, *Stone GH–112*	epigeal	1-gap	2-trace
Engelhardia mexicana	Seedlings, *Stone 2143*	hypogeal	1-gap	3-trace
Engelhardia pterocarpa	Seedlings, *Stone 1016A*	"	1-gap	3-trace
Alfaroa costaricensis	Seedlings, *Stone 2156*	"	1-gap	3-trace

* Voucher specimens have been deposited in the Herbarium of Duke University.

FIGURES 1–7. Seedlings and cotyledonary nodes of Juglandaceae. 1, seedling of *Platycarya strobilacea* with epigeous cotyledons, × 1.5. 2, one-gap two-trace node characteristic of seedlings drawn in 1, 3, and 4. 3, seedling of *Pterocarya stenoptera* with epigeous cotyledons, × 0.4. 4, seedling of *Engelhardia roxburghiana* with epigeous cotyledons, × 0.7. 5, seedling of *Alfaroa costaricensis* with hypogeous cotyledons, × 0.4. 6, one-gap three-trace node characteristic of

deeply bilobed, and, in contrast to *Platycarya*, each of the primary lobes is again deeply and essentially equally bifurcated (FIGURE 3). The cotyledonary node of *P. stenoptera* is unilacunar two-trace (FIGURES 2, 18) as Davey (1916) reported for *P. rhoifolia*. In five of eight nodes examined a small central trace was situated between the main pair (FIGURE 17) but in only one case did the third trace pass into the cotyledon as a separate strand. Generally it fused with the lateral traces, or with the stelar tissue adjoining the gap, or terminated in the cortical tissue.

The genus *Juglans* is divided into three sections and twenty species with representatives in both the New and Old World (Manning, 1961). The genus is closely related to *Pterocarya* but in general has more advanced features. The fewer-flowered inflorescence of *Juglans* is associated with the development of heavy fruits with thick shells and an indehiscent husk. The large cotyledons serve as food storage organs and remain enclosed in the shell below ground at germination (Lubbock, 1892; Rowlee & Hastings, 1898; Davey, 1916; Pammel & King, 1918; Henrotin, 1933; Nast, 1941; Gravis, 1943; FIGURE 8). The cotyledonary node of *J. ailantifolia* Carr. (= *J. sieboldiana*, Davey, 1916) is basically trilacunar (FIGURE 9), although bilacunar nodes do occur. Occasionally both types are found in the same seedling (FIGURES 21, 22). Nast (1941) reports that *J. regia* L. has a four-gap four-trace cotyledonary node, similar to some seedlings of *Carya*.

The genus *Carya* also has representatives in southeastern Asia and the eastern part of Canada, the United States, and Mexico. By all standards it is the most advanced member of the family. In the aspect of seeds and seedlings the species of *Carya* are similar to certain species of walnuts. The fruits are large, with a very hard shell and thin to thick dehiscent husk. As in *Juglans* the fruits are adapted to animal dissemination. The heavy seeds display hypogeal germination (Rowlee & Hastings, 1898; Pammel & King, 1918; FIGURE 10) and the cotyledons remain in the shell. Considerable variation was found in the number of traces supplying the cotyledons. *Carya aquatica* (Michx. f.) Nutt. has multilacunar cotyledonary nodes with six gaps and six traces (FIGURES 11, 23). *Carya cordiformis* (Wang.) K. Koch was found to have a four-gap four-trace cotyledonary node (FIGURE 12), although Davey's report (1916) of hexarch vascular poles in the hypocotyl indicates that three-gap three-trace nodes might also be common. Davey also reported octarch vascular poles in the hypocotyl of *C. illinoensis* (Wang.) K. Koch (= *C. olivaeformis*, Davey, 1916) so the seedlings probably have a four-gap four-trace node. *Carya laciniosa* (Michx. f.) Loud. has extremely large fruits with multilacunar cotyledonary nodes supplied with five to six gaps and traces (FIGURE 13). *Carya ovata* (Mill.) K. Koch is a close relative of *C. lacin-*

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seedlings drawn in 5 and 7. 7, seedling of *Engelhardia pterocarpa* showing hypogeal germination, × 0.4.

FIGURES 8–14. Seedlings and cotyledonary nodes of Juglandaceae. 8, seedling of *Juglans ailantifolia* showing hypogeal germination, × 0.4. 9, bilacunar and trilacunar cotyledonary nodes of *Juglans ailantifolia*. 10, seedling of *Carya aquatica* with hypogeous cotyledons, × 0.4. 11, six-gap six-trace node of *Carya aquatica*. 12, four-gap four-trace node of *Carya cordiformis*. 13, pentalacunar and hexalacunar nodes of *Carya laciniosa*. 14, trilacunar nodes characteristic of *Carya ovata* and *C. tomentosa*.

iosa but has trilacunar cotyledonary nodes (FIGURE 14), as does the tetraploid *Carya tomentosa* Nutt. (FIGURE 14).

The genus *Engelhardia*, as recognized by Jacobs (1960) and Manning, (1966), has two Old World sections and a New World section distributed from southern Mexico to Costa Rica. The unifying and distinctive feature of this genus is the elongate pistillate inflorescence bearing dense clusters of 3-winged fruits. While the fruits vary greatly in size they all seem to have aerodynamic stability for wind dispersal. Germination is of two sorts. Both Old World sections have members with epigeal germination (sect. ENGELHARDIA, *E. serrata* Bl. [Jacobs, 1960]; *E. apoensis* Elmer ex Nagel; sect. PSILOCARPEAE, *E. roxburghiana* Wall., FIGURE 4). Species of section OREOMUNNEA, on the other hand, display the hypogeal germination pattern that characterizes all other New World taxa of Juglandaceae (FIGURE 7). The seedlings examined have nodal patterns correlated with the type of germination. *Engelhardia roxburghiana* (FIGURES 2, 16) has epigeal germination and a one-gap two-trace cotyledonary node similar to *Platycarya* and *Pterocarya*. Both *E. mexicana* Standley (FIGURE 19) and *E. pterocarpa* (Oersted) Standley (FIGURES 6, 7) have hypogeal germination with a one-gap three-trace node.

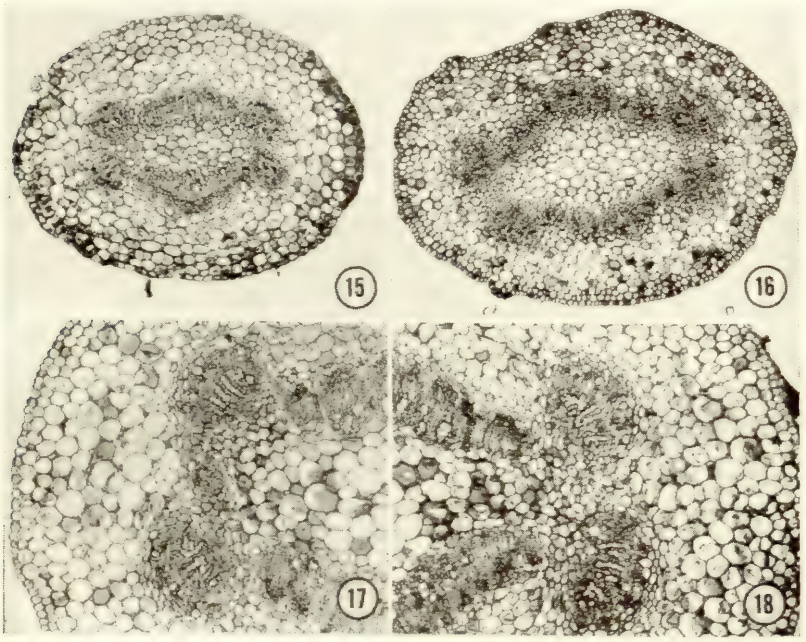
The small genus *Alfaroa* is confined to the premontane rain forests (Holdridge, 1964) of southern Mexico, Central America, and northern Colombia. It has many vegetative and reproductive characters in common with *Engelhardia* sect. OREOMUNNEA but differs markedly in those of the fruit. The well-developed wings of *Engelhardia* fruit appear only as small basal tabs on fruits of *Alfaroa*, while the floral tissue enlarges to form a thin to thick indehiscent husk. There is a striking superficial resemblance between the fruits of *Juglans* and *Alfaroa*. *Alfaroa costaricensis* Standley has hypogeal germination (FIGURE 5) and a one-gap three-trace cotyledonary node (FIGURES 6, 20).

A common pattern of five vascular bundles is seen in the cotyledonary petioles in the Juglandaceae (Stone, in press). In *Pterocarya* the veins of the lamina form three double-stranded traces in the distal end of the petiole (FIGURE 24). Near the middle of the petiole the central trace separates, one half merging with each lateral trace. The two resulting bundles in the proximal end of the petiole enter the stele at a single gap. In *Platycarya* the levels of branching and fusion are slightly different but the basic pattern is the same. Davey (1916) reports three double-stranded traces in the petioles of *Carya cordiformis* (= *C. amara* Nutt.), *Juglans nigra*, *J. ailantifolia*, *J. cinerea*, and *J. regia*. In these species the three traces do not anastomose in the proximal end of the petiole but enter the stele at three separate gaps. The four-gap four-trace node of *J. regia* reported by Nast (1941) is a variation of the same pattern. Again, three double-stranded traces are formed in the petiole but the central trace divides in two in the basal end of the petiole and four traces enter the stele at four

gaps. In a cleared cotyledon of *Juglans olanchana* Standley the double central trace fused with one of the lateral bundles entering the bilacunar node (FIGURE 25).

DISCUSSION

In 1914, after a broad survey of the angiosperms, Sinnott proposed the trilacunar node as the primitive type from which unilacunar and multilacunar nodes were derived. With this pattern as the basis, subsequent investigators have used nodal anatomy as an aid in determining the systematic position of families within orders and genera within families (Bailey & Howard, 1941; Money, Bailey & Swamy, 1950; Swamy & Bailey, 1950; Canright, 1955). By 1955 sufficient information had accumulated to spark a reevaluation of Sinnott's sequence of nodal types (Marsden & Bailey, 1955; Canright, 1955). The prevalence of the unilacunar two-trace node in lower vascular plants, primitive woody Ranales, and in the cotyledonary node of angiosperm seedlings has led to the recognition of this nodal pattern as the basic type. This revised concept of nodal evolution has been generally accepted (Foster & Gifford, 1959; Carlquist, 1961), although perhaps with some reservations.



FIGURES 15–18. Cotyledonary nodes of epigeous Juglandaceae. 15, one-gap two-trace node of *Platycarya strobilacea*, × 47. 16, one-gap two-trace node of *Engelhardia roxburghiana*, × 55. 17, one-gap two + one-trace node of *Pterocarya stenoptera*, × 55. 18, one-gap two-trace node of *Pterocarya stenoptera*, × 55.

Recently the validity of the Marsden-Bailey model of nodal evolution has been questioned (Pant & Mehra, 1964; Benzing, 1967; and Cronquist, 1968). In particular, Benzing's studies on foliar nodes of the woody Ranales suggest that those families with unilacunar two-trace nodes are characterized by specialized floral features and derived decussate phyllotaxy (i.e. Chloranthaceae, Monimiaceae, Austrobaileyaceae). Also, as Carlquist (1961) has noted, it is curious to find the unilacunar two-trace condition in foliar nodes of such advanced families as the Labiatae (leaves opposite or whorled), Solanaceae (leaves alternate or becoming opposite at or near the inflorescence: Lawrence, 1951), and Verbenaceae (leaves opposite or whorled). "The possibility that two-trace unilacunar nodal anatomy evolved in association with opposite phyllotaxy from an ancestral condition characterized by alternate arrangement . . . is quite likely" (Benzing, 1967).

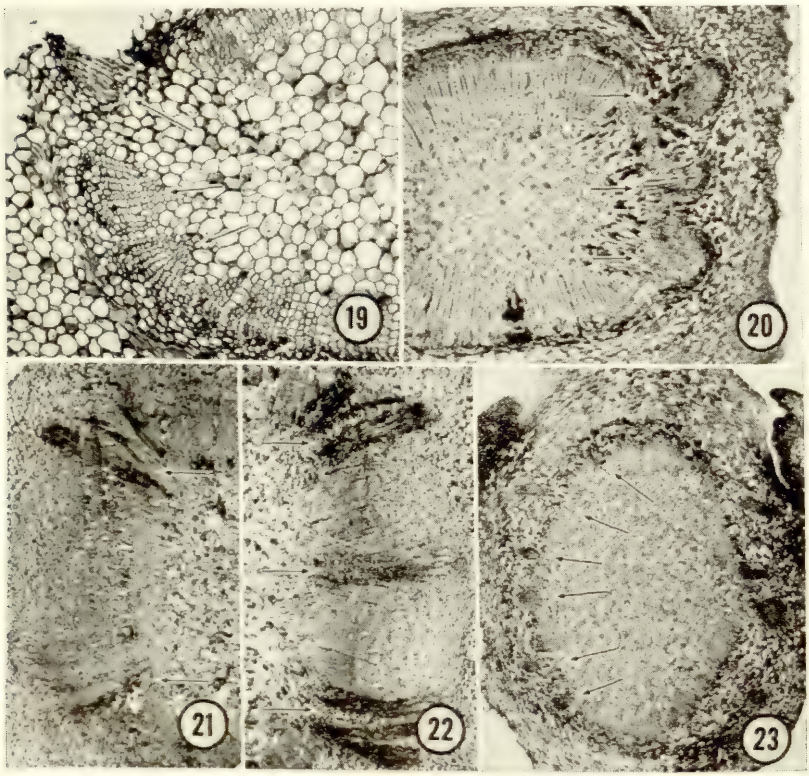
Of course the Marsden and Bailey model of nodal evolution does not rely exclusively on the patterns of foliar nodes. One of the mainstays of the argument rests on the relatively conservative nature of the cotyledonary node. In a survey of the seedlings of 99 families of dicotyledons, Bailey (1956) found that 77 percent had an even number of vascular strands at the cotyledonary node, and 60 percent were unilacunar two-trace. The trilacunar cotyledonary node was found in about 10 percent of the species but not a single multilacunar attachment was encountered; hence the conclusion that cotyledonary nodal anatomy is more conservative than foliar and the unilacunar two-trace node is primitive. Benzing (1967) points out, and rightly so, that "The anatomy of cotyledonary nodes does not necessarily reflect ancestral conditions in the mature stem; the unique seedling morphology and decussate insertion of the cotyledons makes this unlikely." If we are able to accept the available information at face value, it seems likely that evolution of the foliar node has progressed independently of the cotyledonary node.

The usefulness of cotyledonary nodal anatomy in phylogenetic studies depends, of course, on its degree of conservativeness. Certainly Bailey's survey (1956) suggests that cotyledonary attachment is conservative, but unfortunately few details are provided on families or species examined and no information on cotyledonary size, position, or activity. This information is relevant because there is circumstantial evidence that relates cotyledonary development to physiological activity of the seedling (Compton, 1912). A rapidly growing seedling with a large cotyledonary food supply or one that has large cotyledons that are photosynthetically active might be expected to have the best developed vascular system (Hill & de Fraine, 1913). Boureau (1954) and Carlquist (1961) note that complexity of vascularization does not parallel size of seedlings, but it must be recognized that vascular supply and seedling demand are relative. Functional significance of vascular supply would lead to adaptive changes that involve both increases and decreases in vascular complexity. *Fitchia*, an exceptional member of the Compositae with enormous epigeous cotyledons and pentalacunar nodes, seems to represent a good example of increased vas-

cularization (Carlquist, 1957). Decreased vascularization associated with reduced functional demand might be the case in two epigeous members of the Fagaceae (Carlquist, 1961, after Gravis, 1943). The large foliaceous cotyledons of *Fagus sylvatica* have multilacunar nodes, whereas the smaller, fleshy green cotyledons of *Carpinus betulus* (Lubbock, 1892) are vascularized with a highly reduced unilacunar system.

The evidence at hand suggests that vascularization of seedlings is comparable to the situation in other parts of the plant. In those groups where selection pressure is intense for a particular characteristic, conservatism is shed. The Juglandaceae offer additional proof of the adaptability of seedling morphology and anatomy.

The basic vascular supply to the cotyledons in the Juglandaceae is relatively uniform. As we have been able to confirm for *Pterocarya*, *Platycarya*, *Juglans*, and *Carya* (Davey, 1916; Nast, 1941), the veins from the



FIGURES 19–23. Cotyledonary nodes of hypogeous Juglandaceae. 19, one-gap three-trace node of *Engelhardia mexicana*, × 104. 20, one-gap three-trace node of *Alfaroa costaricensis*, × 75. 21, two-gap two-trace node of *Juglans ailantifolia*, × 10. 22, three-gap three-trace node of *Juglans ailantifolia*, × 10. 23, six-gap six-trace node of *Carya aquatica*, × 15. Vascular traces marked with arrows.

four cotyledonary lobes merge to form five traces in the distal region of the petiole. In *Platycarya* and *Pterocarya* the central double strand fuses with the two laterals to enter the single gap as two compound traces (FIGURE 24). The bilacunar, trilacunar, and multilacunar nodes of *Juglans* and *Carya* probably result from varying degrees of separation and fusion of the double-stranded units (FIGURE 25). The presence of two to a maximum of six gaps supports this interpretation. The spatial separation of the strands is certainly correlated with the larger size of the nodal region and petiole base. Sinnott (1918) has noted similar variations of the double-stranded central trace in other angiosperms. In the hypogeal seedlings of *Carya* and *Juglans*, and to a lesser extent the New World *Engelhardia* and *Alfaroa*, the cross-sectional area of the vascular bundles is noticeably larger than in the epigeal seedlings. This may well be the result of extensive branching of the vascular system in the massive cotyledons of the hypogeal forms (Stone, in press).

It is at the level of the cotyledonary node that the Juglandaceae show such remarkable diversity of vascular patterns, patterns which may be correlated with seed and seedling size. The small seedlings of *Platycarya* (FIGURE 1), *Pterocarya* (FIGURE 3), and *Engelhardia* (sect. ENGELHARDIA and sect. PSILOCARPEAE; FIGURE 4) have epigeous, foliaceous cotyledons with unilacunar two-trace nodes. The larger hypogeal seedlings of *Engelhardia* sect. OREOMUNNEA (FIGURE 7) and *Alfaroa* (FIGURE 5) are unilacunar three-trace; those of *Juglans* (FIGURE 8) and *Carya* (FIGURE 10) have bilacunar, trilacunar, and multilacunar nodes.

These three levels of nodal complexity generally parallel proposed generic phylogenies derived from independent assessment of wood (Heimsch & Wetmore, 1939), inflorescences (Manning, 1938), flowers (Manning, 1940, 1948), pollen (Whitehead, 1965), and fruits (Leroy, 1955). The genus *Engelhardia*, for example, as viewed by Manning (1966), has three sections: sect. ENGELHARDIA and sect. PSILOCARPEAE are Old World; sect. OREOMUNNEA is New World. *Engelhardia roxburghiana* of sect. PSILOCARPEAE, with its primitive pollen and characteristics of both sect. ENGELHARDIA and sect. OREOMUNNEA, has been suggested as the intermediate or connecting link (Manning, 1966; Stone, 1968). Information from cotyledonary nodal anatomy is compatible with such a sequence. The Old World sections of *Engelhardia* both have primitive epigeal germination with unilacunar two-trace nodes. The New World sect. OREOMUNNEA is a derived member with hypogeous cotyledons and unilacunar three-trace nodes. The end point in this series is the genus *Alfaroa*. By all standards it is closely related to *Engelhardia* sect. OREOMUNNEA but unlike the Engelhardias it has a large, wingless, nutlike fruit (Manning, 1949, 1959; Stone, 1968). In the few species we have examined, *Alfaroa* has hypogeal germination and unilacunar three-trace nodes similar to *Engelhardia* sect. OREOMUNNEA.

The increase in nodal complexity is evident also in the *Pterocarya-Juglans* alliance. *Pterocarya*, which is generally acknowledged to be the more primitive of the two (Manning, 1938, 1940, 1948, 1949; Whitehead,

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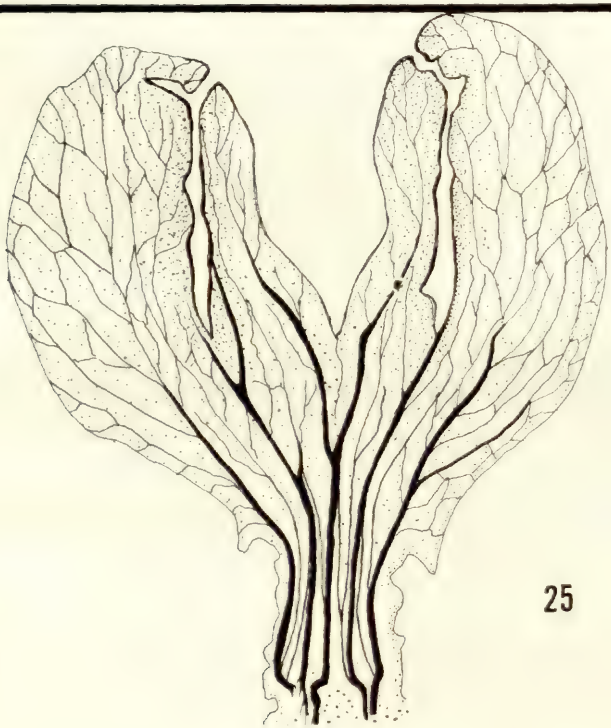

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1965), has small 2-winged fruits with epigeal germination and unilacunar two-trace nodes. *Juglans*, on the other hand, is noted for its large, wingless fruits, hypogeous cotyledons, and trilacunar three-trace cotyledonary nodes.

The genera *Platycarya* and *Carya* are more difficult to place on the phylogenetic tree. *Platycarya* has primitive floral features (Manning, 1938, 1940, 1948) but advanced wood (Heimsch & Wetmore, 1939) and distinctive pollen with pseudocolpi (Whitehead, 1965). This monotypic genus is usually treated as an isolated element derived from *Engelhardia* stock. Seedling morphology is consistent with this view. The fruits are small with minute wings and the seedlings have epigeous cotyledons and unilacunar two-trace nodes similar to those of *Engelhardia* and *Pterocarya*. Without doubt *Carya* is the most advanced member of the family. The fruits are large, germination is hypogeal, and cotyledonary nodal anatomy ranges from three-gap three-trace to six-gap six-trace. The general similarity of fruit and seedling characteristics shared with *Juglans* suggest a close relationship, but the totality of evidence (Hjelmqvist, 1948; Manning, 1948, etc.) seems to favor the idea that *Carya* and the *Pterocarya-Juglans* alliance had separate evolutionary pathways stemming from the *Engelhardia* plexus (Whitehead, 1965).

The remarkable diversity of cotyledonary nodal anatomy may at first seem inconsistent with the view that the genera of Juglandaceae comprise a very natural plant family (Lawrence, 1951). On closer inspection, however, it is apparent that the nodal attachments are part of the syndrome of characters associated with patterns of adaptive radiation. Vegetatively the family has been relatively conservative. All members are trees of temperate or cool tropical areas with pinnately compound, resin-dotted, aromatic leaves (Manning, 1961). Diversification of the genera has proceeded through the elaboration and adaptation of flowering and fruiting structures. Modifications of the inflorescences, staminate flowers, and pistillate flowers appear to be refinements for wind pollination and seed dissemination. The primitive fruits were probably small and had minute wings like those of *Platycarya* (Manning, 1940) or *Rhoiptelea* (Manning, 1961). From this stage of development fruit dispersal by wind and animals evolved along several generic lines. In *Engelhardia* the development of larger wings led to larger fruits, and eventually a shift from epigeal to hypogeal germination with a concomitant increase in vascular complexity. Once hypogeous cotyledons and complex nodes were fixed the exploitation of new niches was pursued in *Alfaroa* by the loss of wings, development of a husk, and increase in size of fruit (Stone, 1968). Similar adoption of even more complex nodes is coupled with the advent of hypogeal germination in *Juglans* and *Carya*. The general pattern of evolution of the juglandaceous seedling shows a one to one correspondence between the adaptation to hypogeal germination and increased nodal complexity. The

FIGURES 24, 25. Drawings of cleared cotyledons of Juglandaceae. 24, vascular anatomy of a one-gap two-trace "cotyledon" of *Pterocarya stenoptera*, × 5. 25, vascular anatomy of a two-gap two-trace "cotyledon" of *Juglans olanchana* (*Stone 2701*), × 3.

enlarged nodal region of hypogeal seedlings may well have been advantageous in overcoming the "spatial and other difficulties in the development of multilacunar nodes where the leaves are opposite" (Bailey, 1956). Thus, the conservatism of seedling anatomy in the dicotyledons may well be related to the constraints placed on nodal development in most groups by the prevalence of primitive, epigeal germination.

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THE VASCULAR SYSTEM IN THE AXIS OF DRACAENA FRAGRANS (AGAVACEAE) 2. DISTRIBUTION AND DEVELOPMENT OF SECONDARY VASCULAR TISSUE

M. H. ZIMMERMANN AND P. B. TOMLINSON

IN THE FIRST PAPER of this series, we described the distribution and origin of primary vascular bundles in *Dracaena fragrans* (L.) Ker-Gawl. (Zimmermann & Tomlinson, 1969). We showed that the principle of primary vascular structure and development in *Dracaena* is similar to that of other monocotyledons we had studied (Zimmermann & Tomlinson, 1965, 1967, 1968). However, like a few other woody monocotyledons, *Dracaena* differs from palms because it has a vascular cambium which produces secondary vascular tissue. In this way *Dracaena* resembles a woody dicotyledon although the secondary tissue produced from the monocotyledonous kind of cambium differs from that of most dicotyledons because it matures as a series of anastomosing vascular bundles within a matrix of secondary parenchyma (Tomlinson & Zimmermann, 1969). In this present paper we examine the distribution and development of secondary tissues and its relation to primary vascular development.

The structural relation between primary and secondary vascular bundles in *Dracaena* was one of the earlier problems of monocotyledonous anatomy to be investigated. It was studied by von Mohl (1824, 1849) and his contemporaries, notably de Mirbel (1845). The observations and interpretations of these early botanists with regard to the development of the *Dracaena* type of stem were inconclusive and often contradictory. Continuity between primary and secondary bundles was indeed described by a number of these early authors and in this sense our own observations can be said to do no more than confirm earlier work. However, we now know that a knowledge of secondary vascular development must be based upon an understanding of primary vascular development within the crown. This information had not been available until our own analysis of the course of procambial strands in the developing crown of *Dracaena* was presented. With this understanding we can now discuss in a meaningful way the distribution of secondary vascular tissues in monocotyledons.

Most of the background information to this paper, including growth habit and general histology of *Dracaena* has been presented in the first paper of this series (Zimmermann & Tomlinson, 1969).

MATERIALS AND METHODS

Sources of materials, methods of sectioning and serial analysis by ciné microphotography have been dealt with in the first paper. The relation between primary and secondary tissues was investigated in the sapling

axis of a plant grown from seed to an overall height of 75 centimeters within three years. During this time it had not flowered, and remained unbranched. The basal 12 centimeters of the aërial stem of this sapling was fixed for investigation.

Outgrowth of lateral buds below a terminal inflorescence and their method of establishing vascular continuity with a parent stem was studied, following a flowering period in December, 1968. Shoots were dissected at intervals after flowering, fixed in FAA, embedded in paraffin and sectioned serially. Detailed analyses of two successive stages were made by the cinematographic method.

DISTRIBUTION OF SECONDARY TISSUE

Establishment growth in seedlings. Most monocotyledons have no secondary growth, and in order to produce a stable axis thickening growth must precede growth in height (Schoute, 1903). In the majority of arborescent monocotyledons, represented by most palms, the leafy

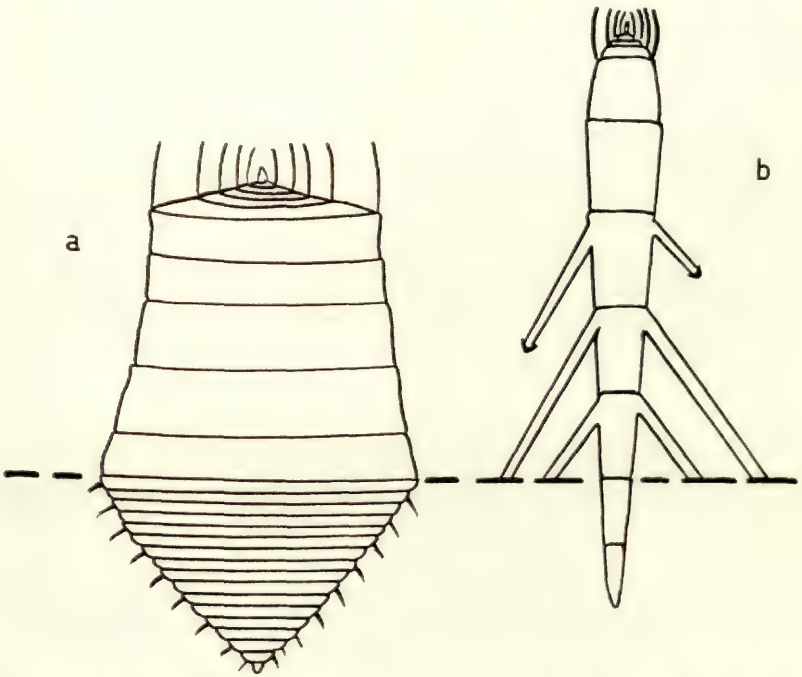

FIGURE 1. Establishment growth in large monocotyledons. 1a. Type found in most palms and other arborescent monocotyledons; the stem widens with short internodes until it has reached the approximate diameter of the adult stem before growth in height begins with longer internodes. 1b. Type found in *Pandanus* and a few palms such as *Socratea*: growth in height begins early, the widening stem is supported by prop roots.

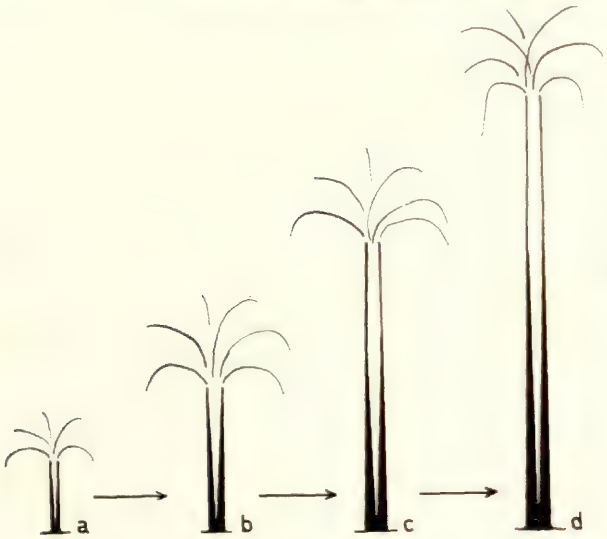

FIG. 2

POST - SEEDLING GROWTH

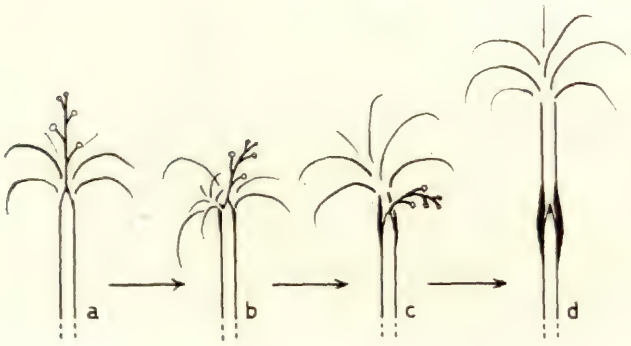

FIG. 3

SYMPODIAL GROWTH

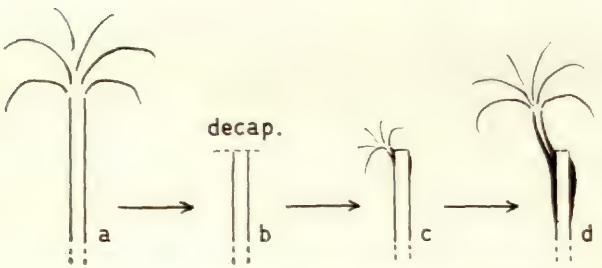

FIG. 4

GROWTH AFTER DECAPITATION

FIGURES 2–4. Distribution of secondary vascular tissue (black) in *Dracaena fragrans*. 2a–d. Establishment growth during the post-seedling stage. Growth in height begins early, the stem increases in width by secondary growth as it grows in height. Secondary vascular bundles are initially produced in close association with primary bundles (FIGURE 2a, b). Eventually, secondary growth is "left

crown of seedlings remains at ground level and enlarges gradually. Growth in height does not begin until crown size and stem diameter have reached that of the adult tree. During this time of "establishment growth" height growth is minimal, internodes are very short, and an underground obconical axis develops (FIGURE 1a). In a few palms (e.g. *Socratea*) and in *Pandanus* establishment growth is associated with growth in height because internodes elongate, but the resulting axis is stabilized mechanically by supporting prop roots (FIGURE 1b). During this period of establishment growth the number of axial vascular bundles increases by a process of growth which has been described for the palm *Rhapis* in one of our earlier papers (Tomlinson & Zimmermann, 1966).

Conifers and dicotyledons do not depend upon primary establishment growth because secondary growth provides for increase in thickness as the stem grows in height. As the tree grows taller its stem thickens proportionally so that mechanical stability is achieved. The seedling growth of monocotyledons of the *Dracaena*-type is similar in this respect.

In *Dracaena*, germination of seeds is hypogeal and is followed by the development of the seedling axis characteristic for monocotyledons. This involves an initial widening of the crown by establishment growth as is shown in FIGURE 1a, and a multiplication of primary vascular bundles which we presume is similar to that described for *Rhapis* (Tomlinson & Zimmermann, 1966) although we have not yet examined this in detail. However, this phase is very short because growth in height begins very early. Establishment growth then continues in a manner reminiscent of dicotyledons, i.e. by secondary stem thickening while the overall height is increasing. This is shown in FIGURE 2a–d. Although this second phase of establishment growth is similar to that in dicotyledons, because it involves the production of secondary tissue, it differs from it in that the number of primary bundles in the shoot also increases (FIGURES 2a, b). We shall discuss later how this is possible. At the moment it is important to state that during the early post-seedling growth secondary vascular bundles are produced in close association with primary growth of the crown region (FIGURE 2a), but at a later stage of shoot growth (FIGURE 2d) primary growth is very similar to that of palms and involves no closely associated secondary bundles. This latter mode of primary growth formed the substance of the first paper of this series (Zimmermann & Tomlinson, 1969).

Establishment growth in older parts of the plant. *Pandanus*,

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behind" (FIGURE 2c, d). 3a–d. Production of secondary vascular bundles following flowering (establishment growth in the sympodium). A terminal inflorescence is produced (FIGURE 3a), declining apical dominance enables a lateral bud to grow out (FIGURE 3b). The outgrowing lateral "has access" to only few primary vascular bundles but regenerates primary vascular tissue (white) by outer (exogenous) vascular bundles which are secondary (black) in their lower part (FIGURE 3b–d). 4a–d. Establishment growth of lateral shoot after decapitation of the parent axis. Regeneration of the primary vascular tissue by exogenous growth produces primary bundles which are secondary (black) in their lower part.

Dracaena and numerous other woody monocotyledons grow sympodially. The primary axis produces a terminal inflorescence. Apical dominance thus declines and one or more of the lateral vegetative buds below the inflorescence grows out. The morphology of this process has been described by earlier botanists, notably by Schoute (1903, 1906), and is summarized in our introductory paper (Tomlinson & Zimmermann, 1969). If more than one lateral bud grows out the axis will fork. It is indeed largely by this mechanism that many monocotyledonous trees become branched. In order to simplify our description, we will consider here a situation in which only one vegetative bud grows out so that the sympodium remains single.

FIGURE 3 illustrates the sympodial growth of a *Dracaena* axis in a simplified manner. In FIGURE 3a the shoot has reached the flowering state. In FIGURE 3b the terminal inflorescence is beginning to age and a lateral bud begins to grow out. Now it is perfectly clear that the inflorescence is supplied by a large number of primary axial bundles but these are "lost" from the sympodium because growth of the inflorescence is determinate. This means that the newly developing vegetative shoot has to undergo a period of establishment growth in order to restore the approximate equivalent number of vascular bundles. In *Dracaena* this process again involves secondary vascular tissue (FIGURE 3c). Hence, at the time the new vegetative crown is fully re-established, the number of primary vascular bundles is fully restored. An unbranched shoot which flowers repeatedly over a period of time acquires a segmented appearance (cf. *Figure 3* in Zimmermann & Tomlinson, 1969). Two points will be important as we discuss secondary growth later in this paper. First, establishment growth of the new vegetative shoot of a sympodium involves secondary vascular tissue. Second, this secondary vascular tissue (shown black in FIGURE 3b–d) is not necessarily continuous with the secondary vascular tissue towards the base of the tree.

The kind of establishment growth found in flowering shoots also occurs in buds released from apical dominance by other ways, as in the decapitation of a shoot (FIGURE 4) or on the upper side of a leaning branch. Photographic illustrations of this kind of shoot are given in Tomlinson & Zimmermann (1969, *Figures 14* and *15*).

Bundle continuity in the post-seedling axis. FIGURE 5 shows longitudinal and transverse sections of the basal portion of a young *Dracaena* plant, drawn to scale. As a result of establishment growth the diameter of the primary vascular cylinder had increased from 2 mm. at ground level to 12.5 mm. at 11 cm. height. An overall conical stem shape was maintained by secondary growth although the primary vascular cylinder itself is an inverted cone. An 8 cm. long piece from between 3 cm. and 11 cm. height was sectioned and analyzed in detail. The results are shown in FIGURE 6. The sections show that the number of primary vascular bundles also increases with height during establishment growth. The diameter of the primary cylinder at the base of the piece shown in FIGURE 6 is about 7.5 mm. and contains 290 primary vascular bundles. At the top, the diameter of the primary vascular cylinder is 12.5 mm. and contains

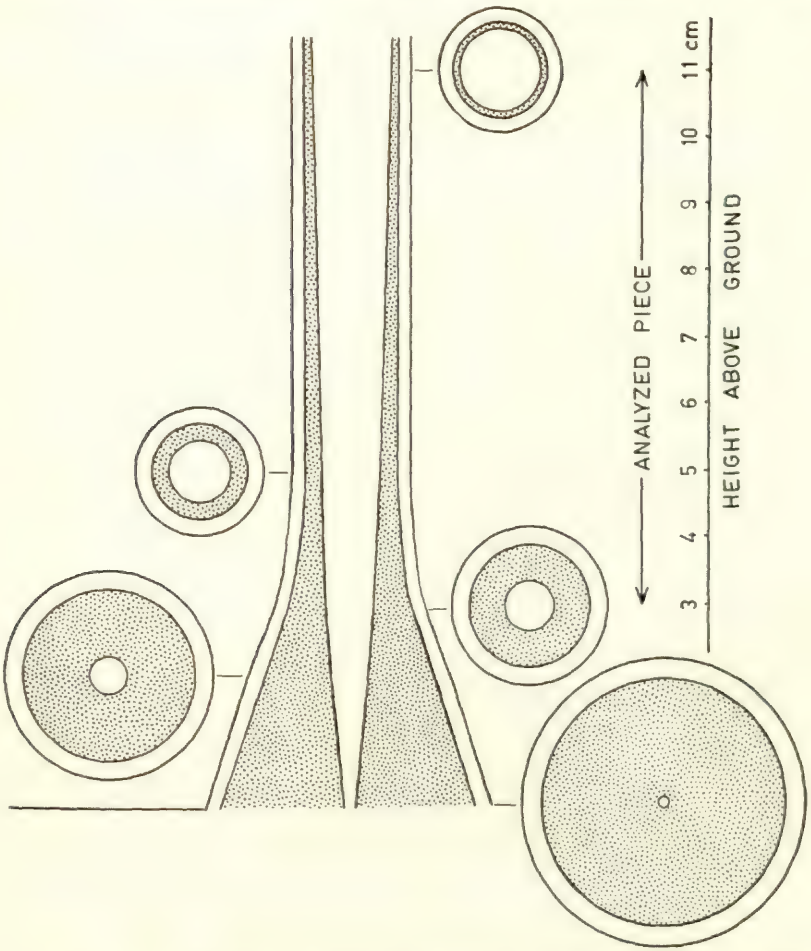

FIGURE 5. Longitudinal and transverse sections (0, 2, 3, 5, and 11 cm. above ground) of the basal part of the analyzed post-seedling stem, showing establishment growth by production of secondary tissue, drawn to scale. The primary stem diameter increases from 2 mm. at ground level to 12.5 mm. at 11 cm. height. The 8 cm.-long piece between 3 cm. and 11 cm. height was used for the analysis shown in FIGURE 6. Secondary vascular tissue is indicated by stippling.

540 primary vascular bundles. Therefore, the question is: where do the 250 new primary vascular bundles come from? Before we can answer this question we may briefly recapitulate our answer to the same problem in the post-seedling stage of *Rhapis*. There we found that the number of vascular bundles increased because each lower leaf trace produced more than one vertical-(axial-)bundle branch. Thus the number of axial bundles is augmented above the departure of each leaf-trace. In *Dracaena*

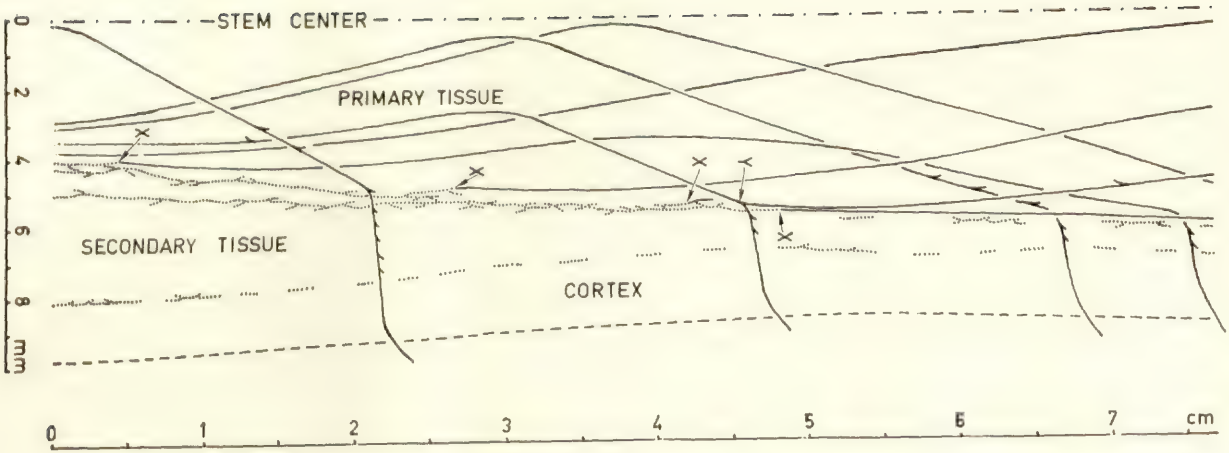

FIGURE 6. Course of vascular bundles in an 8 cm.-long piece of a stem produced by post-seedling establishment growth. Only the central part of the primary stem grew endogenously as do palms. An example of an axial-(vertical-)bundle branch resulting from this kind of growth is shown at Y. Establishment growth (increase in number of primary vascular bundles) is by exogenous growth. Examples of these exogenous (outer) bundles are secondary in their lower part. Primary bundles are shown as solid black lines, secondary bundles as dotted lines. The point of transition from primary to secondary is marked by an arrow at X. Note that all bundles are shown in a single radial plane. The axis is foreshortened about twice.

it is probable that this type of primary establishment growth takes place during the very early phases of seedling growth. Morphological evidence suggests this, although we have not yet analyzed such early stages anatomically. Post-seedling establishment growth of the axis shown in FIGURE 6 is very different and involves secondary vascular bundles. It can be seen in FIGURE 6 that some of the primary bundles of the upper part of the stem are continuous as secondary bundles in the lower part. This is why there are more primary bundles in the upper stem part. The developmental significance of this finding will be discussed later, after the anatomical situation has been described in more detail.

FIGURE 6 is based upon accurate measurements of bundle positions in a young post-seedling axis. As in previous publications radial distances from the stem center are shown regardless of the side of the stem on which they are located. In other words, the whole stem is represented in a single radial plane. One bundle is shown which is entirely primary (FIGURE 6, at Y), three bundles (and a short section of a fourth one) are shown which are primary in their upper part and secondary in their lower part (FIGURE 6, at X). The bundles in FIGURE 6 were plotted on graph paper while being followed individually through a series of transverse sections. Followed towards the base of the stem each approaches the periphery of the primary vascular cylinder and "becomes" a secondary bundle. When followed further down as a secondary bundle their identity was maintained, but only in an arbitrary way, because secondary bundles anastomose extensively.

When the analytical film of the axis used to produce FIGURE 6 is projected so that bundles are followed downwards, one observes that all peripheral primary bundles "sink" into the secondary vascular cylinder, thus "becoming" secondary vascular bundles. When projected in reverse (upwards), secondary bundles "emerge" as primary ones and "move" towards the stem center. FIGURE 7 illustrates four positions of the same vascular bundle at the point of transition. At the highest level (FIGURE 7a) the bundle is collateral (primary) in the distribution of its vascular tissues; at the lowest level (FIGURE 7d) it is amphivasal (secondary) and at intermediate levels (FIGURE 7b, c) an "intermediate" condition can be recognized. These indicate that part of the vascular differentiation within a procambial strand was carried out at a primary phase of growth and completed in a secondary phase.

Bundle continuity in older stem parts. Establishment growth of an outgrowing lateral bud following decapitation of the parent stem (FIGURE 4a–d) is anatomically very similar to that of the post-seedling stem. The secondary bundles are continuous from the daughter into the parent axis. They extend down and around the parent axis in a basal direction. In this type of union it is important to realize that secondary bundles are not continuous with primary ones at their lower extremity. They anastomose extensively among themselves, but as one descends the secondary vascular cylinder gets thinner and finally disappears almost entirely. Vascular continuity between this more recent secondary cylinder and the primary

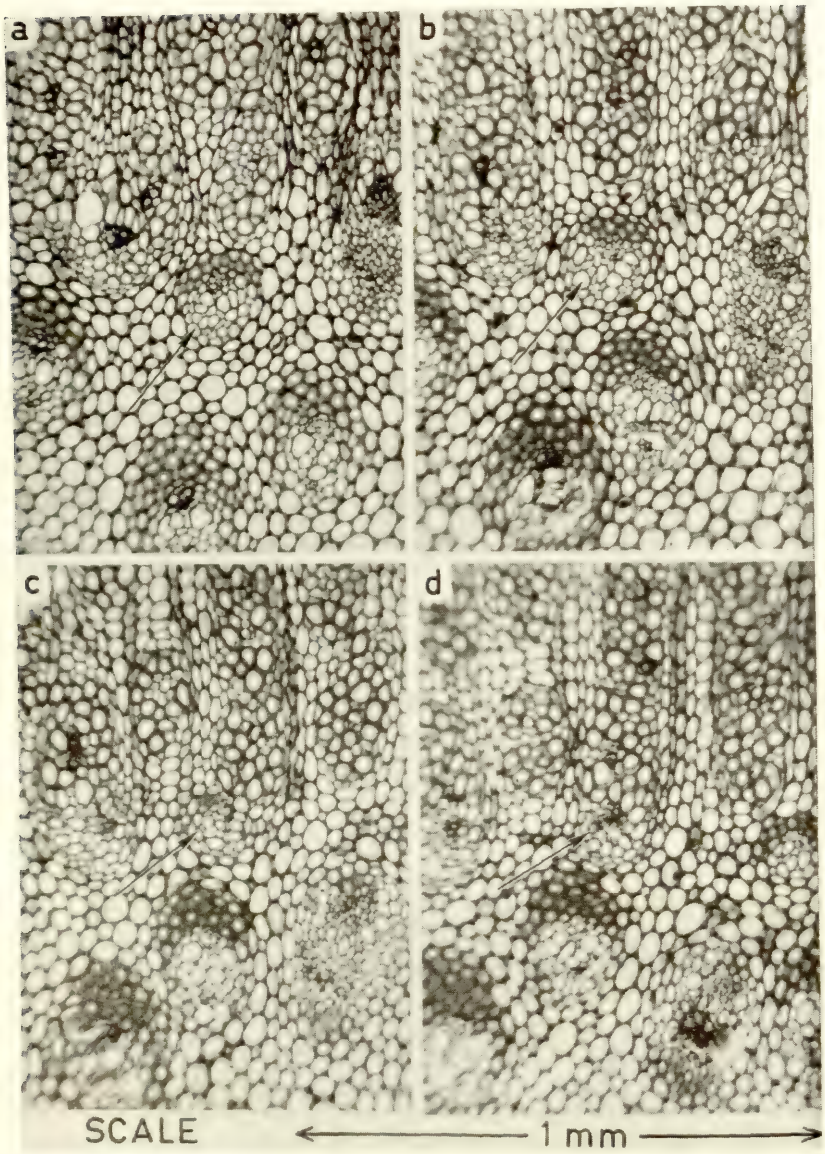

FIGURE 7. A single exogenous vascular bundle (arrow) shown in the area of transition from primary to secondary tissue. In the highest position (FIGURE 7a, 4.8 mm. above the bottom section, FIGURE 7d) the bundle is entirely primary. In the bottom section (FIGURE 7d) it is entirely secondary. Intermediate positions are seen in FIGURE 7b (2.8 mm. above 7d) and FIGURE 7c (1.6 mm. above 7d).

cylinder below is given by radially-running leaf traces which connect to the secondary bundles via short upwardly-directed bridges. Leaf traces continue to elongate radially as long as leaves are still attached to the stem. We do not yet know if their elongation continues after the leaves have fallen off the stem.

We assume that the attachment of lateral outgrowing vegetative buds on the upper side of leaning stems (illustrated in *Figure 15*, Tomlinson & Zimmermann, 1969) is similar to that after decapitation, but we have not yet investigated this situation in detail.

The vascular anatomy of renewal shoots of a sympodial branch is somewhat more complicated. Though we have found, without question, the same basipetal transition of primary into secondary vascular bundles, there are many primary bundles of the daughter shoot which are continuous with *primary* bundles of the mother shoot. This means, of course, that growth of the lateral shoot begins sufficiently early that it is possible for numerous primary bundles of the branch to develop in continuity with primary bundles of the parent shoot. For this reason, there is no sharp distinction between primary and secondary vascular tissues at the level of union when maturation is complete. This contrasts with the sharp boundary between primary and secondary vascular tissue in both the post-seedling and decapitated axis.

LEAF AND BUD TRACE

Foliage leaves in *Dracaena fragrans* are long lived, and can persist for two to three years as functional assimilating organs. All leaves subtend a bud, which remains minute and strongly suppressed, but retains its ability to grow as can be seen in decapitated or leaning shoots. Buds are first recognizable as a meristem in the axil of a leaf in position P15 and bud traces are differentiated at position P16. These traces may be satellites (branches from a major leaf trace) or axial bundles directed into the bud (Zimmermann & Tomlinson, 1969, p. 381). Bud traces, although few and small, are long persistent.

Both foliage leaves and buds in older stems are connected across the secondary cylinder by a series of traces which owe their continuity with the central cylinder to their primary origin. Traces are not ruptured by the activity of the cambium which they cross and it is, therefore, of some interest to understand how they can retain a translocating function across a zone of tissue which increases in thickness continually by meristematic activity. The mechanism is simple and not essentially different from the development of leaf traces within the basal meristems of leaves in all large monocotyledons. Continuity of conducting tissues along the trace is maintained by the continued differentiation of extensible elements of xylem and phloem.

Traces are more or less horizontal within the zone of secondary tissue. Within the cambial zone undifferentiated elements persist around the trace. These cells are somewhat longer than the cambial elements proper which,

together with recent cambial derivatives, make up the cambial zone. Growth in length of the trace, to accommodate for secondary increase in the stem diameter, is the result of occasional vertical divisions in these undifferentiated initials (i.e. divisions transverse to the long axis of the leaf trace). Other divisions are horizontal (the new cell wall is parallel to the long axis of the trace) so that the trace grows in thickness. Existing protoxylem and protophloem elements are eventually ruptured by the extension

FIGURE 8. Tangential section through a stem of *Dracaena fragrans* outside the secondary vascular tissue. A median leaf trace (LT) is cut transversely, above it numerous provascular strands (two of them marked with arrows), connecting a dormant axillary bud with the primary vascular tissue.

of the trace but new ones are continually generated to take their place. The mechanism whereby these new elements are differentiated has not been studied in complete detail. The trace always includes much more xylem than phloem, the latter is most easily recognized by the collapsed elements on the lower side of the trace which stain densely with haematoxylin. It is not known if new conducting elements are added entirely from the surrounding cells, or from the undifferentiated cells between xylem and phloem, or from both sources. These details have not been sought. A group of (still procambial) bud traces of a dormant bud and the median leaf trace of the supporting leaf are shown in a tangential section through the secondary cortical tissue in FIGURE 8.

DISCUSSION

Before we discuss the origin of vascular bundles which are primary in their upper and secondary in their lower part, we must recapitulate the principle of development of the vascular pattern of those monocotyledonous plants which have only primary bundles. A description of this has appeared in print for three species, namely *Rhapis excelsa* (Zimmermann & Tomlinson, 1967, see *Figure 2* therein), *Prionium serratum* (Zimmermann & Tomlinson, 1968, *Figures 14* and *17*) and *Dracaena fragrans* (Zimmermann & Tomlinson, 1969, *Figure 13*). In these papers it has been shown that monocotyledonous vascular bundles originate as branches of leaf traces and grow upwards into a meristematic region, immediately below the shoot apex proper, which we have called the cap. The upper end of a potential vascular bundle in the cap remains undetermined until it is connected to a newly differentiating leaf trace associated with a young leaf primordium. Leaf traces which connect to a potential bundle in the cap center become major bundles, leaf traces which appear during a later stage of leaf-primordium development link with a potential bundle at the cap periphery and thus give rise to a minor bundle with a shorter leaf-contact distance and a more limited radial penetration. This pattern of vascular development is typical and unique for monocotyledons, as far as we know, as it leads to what we call an "inner" (endogenous) vascular system. Additional new leaf traces may subsequently arise outside the cap at a point where no free upper ends of vascular bundles are available. In *Rhapis* and *Prionium* these late-differentiating leaf traces become cortical bundles and end blindly below, sometimes (as in *Rhapis*) anastomosing among themselves. This suggests that there is no physiological mechanism available to "propagate" these bundles.

In *Dracaena*, on the other hand, which has a vascular cambium, such late-appearing ("outer" or exogenous) leaf traces can continue to grow below as secondary vascular traces since there is a vascular cambium available whereby they can be "propagated." This pattern is more like dicotyledonous vascular development and fundamentally different from the "normal" monocotyledonous development of the "inner" vascular system. This developmental pattern in the young sympodial branch pro-

vides an easy and, indeed, the only seemingly possible explanation of primary bundles which are continuous below as secondary bundles. When this situation became clear it lead to the postulate that secondary bundles of *Dracaena* are homologous with the cortical bundles of *Rhapis* and *Prionium*. This, in turn, necessitated the prediction that monocotyledons with secondary growth have no cortical bundles. Examination of sections of a number of species representing genera in the Agavaceae (*Agave*, *Beaucarnea*, *Cordyline*, *Dasylirion*, *Pleomele*, *Yucca*; the Liliaceae (*Aloë*); and the Xanthorrhoeaceae (*Lomandra*, *Xanthorrhoea*) in the microslide collection of one of us (P.B.T.) showed that the prediction was indeed supported. The reverse is not necessarily true, however, because we do know of monocotyledons (e.g. certain Bromeliaceae) in which there is no cortical system, but neither is there a secondary vascular system.

In summary, our investigations so far suggest that monocotyledons possess two patterns of vascular development, an inner one (such as the central vascular system of palms) and an outer one which is represented by a system of cortical fibrous bundles in *Rhapis* and *Prionium*, but in *Dracaena* includes some of the primary bundles (the more peripheral ones in regions of establishment growth) and all the secondary bundles. This last statement needs qualification. We realize that secondary vascular bundles *can* grow in *Dracaena* without direct contact with the crown. Such a situation exists in the basal part of the stem as shown in FIGURE 2c,d. Secondary tissue here "creeps" up on the stem by progressive acropetal development. We know no more about how this vascular development is regulated than we know how vessel development at the base of a ring-porous dicotyledonous tree is regulated.

We realize that many questions are still unanswered. It will be necessary to find out how sharply definable the two patterns of development are in *Dracaena*. We have seen very clear-cut examples of both types, but we have the impression that a sharp line cannot always be drawn between the two. Ultimately, the problems of developmental physiology will have to be studied. Vascular strands must always develop between two physiological poles. The positional arrangement of these poles is much more complicated in monocotyledons than in dicotyledons. In spite of all these open questions, however, we feel that *Dracaena* has brought us considerably closer to the understanding of monocotyledonous growth.

SUMMARY

In the region of establishment growth some of the primary vascular bundles of *Dracaena fragrans* are continuous below with secondary vascular bundles. In terms of development this can be accounted for by late differentiating leaf traces which fail to make contact with the meristematic cap of the developing crown. Unlike the corresponding bundles in palms which form a feebly developed cortical system, these bundles in *Dracaena* continue their differentiation in association with the secondary vascular cambium as secondary vascular bundles. The cortical system of *Rhapis*

and *Prionium* is thus homologous with the secondary vascular system of *Dracaena*. Further evidence in support of this comes from the observation that all monocotyledons with secondary vascular tissues which have been examined lack an independent cortical system.

ACKNOWLEDGMENTS

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RELATIONSHIPS IN THE PIRIQUETA CAROLINIANA-P. CISTOIDES COMPLEX (TURNERACEAE)

ROBERT ORNDUFF

IN ASSOCIATION WITH an investigation of the breeding systems of *Piriqueta caroliniana* (Walt.) Urban sensu lato (Ornduff & Perry, 1964) and *P. cistoides* (L.) Griseb. (Turneraceae), I have carried out a crossing program to determine whether the conspicuous morphological variation within these species is associated with (or maintained by) inter- or intraspecific barriers to crossing or with hybrid sterility. This paper presents the results of the hybridization program and briefly discusses some of the evolutionary and taxonomic implications of these results. Many of the variants in each species have been accorded taxonomic recognition by other authors. In the following paragraphs, however, the use of binomials or of varietal names is one of convenience in referring to the morphological variants and is not a reflection of taxonomic decisions that I have made in the group. Both species discussed in this paper are in need of a taxonomic revision that must utilize a wider range of techniques than those I have used here.

I am indebted to W. R. Anderson, W. R. Ernst, F. W. Martin, and J. W. Purseglove for their generous assistance in providing seeds of *Piriqueta cistoides* and to J. D. Perry for providing the results of his preliminary investigations of the *P. caroliniana* group. Much of this work was carried out at the Department of Botany, Duke University, and was supported in part by research grants from the National Science Foundation and Associates in Tropical Biogeography at the University of California.

Piriqueta caroliniana is usually a perennial herb which ranges along the Coastal Plain from South Carolina southward through Florida to Cuba and Haiti (Urban, 1883; Small, 1933; Brizicky, 1961; Ornduff & Perry, 1964). A few collections referred to this species also have been made in scattered localities in Brazil, Venezuela, and Colombia (Urban, 1883). The species is absent from the Lesser Antilles. *Piriqueta caroliniana* occurs in somewhat sandy soil of dunes, grassy areas, or open woodlands, and, although it seems able to tolerate ecological disturbance such as fire, lumbering, or grazing, it is not an invasive weed.

Urban (1883) recognized six varieties of *Piriqueta caroliniana* which differ largely in pubescence and foliar characters. Three of the varieties occur in the United States, although only one is restricted to this country. Small (1903, 1933) recognized four species of *Piriqueta* in the United States that are distinguished primarily by characters of the pubescence. Three of these species occur only in Florida. In contrast, Brizicky (1961) recognized only a single species (*P. caroliniana*) with five varieties in the United States and suggested that the "entire genus is much in need of a modern taxonomic revision, and field observations, culture experiments,

and cytogenetic studies are needed to determine the status (probably intraspecific) of the variants in our area."

A close relative of *Piriqueta caroliniana* is *P. cistoides*, a widely distributed rather weedy plant that occurs in the Greater Antilles and the Lesser Antilles, and also ranges from Mexico through Central America into Brazil (Urban, 1883). Although described as an annual, some plants of this species will continue to flower for at least three years in cultivation.

Piriqueta cistoides is variable throughout its range. Urban (1883) recognized eight varieties in this species. *Piriqueta cistoides* var. *cistoides* is the most widely distributed and occurs almost throughout the range of the species; in pubescence characters it resembles *P. caroliniana* var. *caroliniana*. Four of the varieties are restricted to mainland South America, one is endemic to Jamaica, and two occur in both the West Indies and on the South American continent. In general, however, subsequent authors (including Urban, 1920) have not recognized infraspecific taxa in *P. cistoides* (e.g., Boldingh, 1913; Fawcett & Rendle, 1926; Standley, 1928; Stahl, 1936; and Alain, 1957).

Piriqueta caroliniana and *P. cistoides* are diploid with $n = 7$ (TABLE 1; Lewis et al., 1962). The most consistent morphological differences between them are floral ones. *Piriqueta caroliniana* has large, distylous, and strongly self-incompatible flowers; *P. cistoides* has small, homostylous, and largely autogamous flowers.

HYBRIDIZATION PROGRAM

A program of artificial inter- and intraspecific hybridizations was carried out with *Piriqueta caroliniana* and *P. cistoides*. Plants of *P. caroliniana* used in this program were referable to each of the morphological variants recognized by Small (1933; TABLE 1). Three of the collections of *P. cistoides* were referable to var. *cistoides*; the Trinidad plants were closest to var. *latifolia* Urb. (TABLE 1). Seeds from South American and Meso-American populations of these species have not been available, and, as a result, this study has been limited to representatives from the southeastern United States and the West Indies.

Artificial hybridizations were carried out in insect-proof cages in the greenhouse. The large, self-incompatible flowers of *Piriqueta caroliniana* were not emasculated prior to hybridization, but the anthers of the small, autogamous flowers of *P. cistoides* were removed before anthesis to prevent self-pollination. Intraspecific interpopulation hybridizations are easily accomplished in *P. caroliniana* and result in a full seed-set. In contrast, the seed-set following such hybridizations within *P. cistoides* is reduced, possibly because of damage to the flowers as a result of removal of the anthers. Interspecific hybridizations were possible only when *P. cistoides* served as the seed parent, indicating the presence of a unilateral incompatibility system. When the hybrids flowered, pollen samples from them

TABLE 1. Origin and chromosome numbers of collections of Piriqueta used in crossing program

TAXON	DESIGNATION	CHROMOSOME NUMBER	ORIGIN
(*P. cistoides* var.)			
cistoides	Dominica	$n = 7$	Dominica, West Indies, *W. R. Ernst 2141.*
cistoides	Jamaica		Kingston, Jamaica, *M. Crosby, H. Hespenheide,* & *W. Anderson 1264.*
cistoides	Puerto Rico		Near Mayaguez, Puerto Rico, *F. W. Martin s.n.*
latifolia	Trinidad	$n = 7$	St. Augustine, Trinidad, *J. W. Purseglove s.n.*
(*P. caroliniana* var.)			
glabrescens	*1519*		Florida. Collier County: east of Monroe Station, *J. D. Perry 1519.*
caroliniana	*6454* [1]	$n = 7$	South Carolina. Orangeburg County: west of Santee.
tomentosa	*6743*		Florida. Hillsborough County: Tampa.
glabrescens	*6746*	$n = 7$	Florida. Collier County: east of Naples.
tomentosa-viridis-glabrescens [2]	*6750*	$n = 7$	Florida. Dade County: southwest of Homestead.
caroliniana	*6752*	$2n = 14$	Florida. Dade County: west of Perrine.
tomentosa-caroliniana [2]	*6754*	$n = 7$	Florida. Dade County: Suniland.
viridis	*6755*	$n = 7$	Florida. Glades County: southeast of Palmdale.
caroliniana	*6758*	$n = 7$	Florida. Highlands County: south of DeSoto City.
caroliniana	*6762*		South Carolina. Jasper County: near Hardeeville.

[1] Collection numbers are those of the author unless otherwise noted.
[2] Population contains plants referable to each taxon or intermediate between the taxa.

were mounted in aniline blue-lactophenol and scored for viability on the basis of their staining reaction (TABLE 2).

RESULTS

Fifteen hybrid progenies of *Piriqueta caroliniana* representing 14 inter-population combinations were obtained (TABLES 1, 2). The average

TABLE 2. **Results of artificial hybridizations of Piriqueta caroliniana and P. cistoides**

CROSS	AVERAGE POLLEN VIABILITY	(RANGE OF POLLEN VIABILITIES; NUMBER OF PLANTS IN PROGENY)
[Intraspecific hybridizations: *P. caroliniana*]		
6454 × *6755* [1]	88	(64–99; 5)
Reciprocal	76	(59–99; 7)
6454 × *6758*	89	(72–100; 5)
6743 × *6746*	90	(75–98; 8)
6743 × *6754*	94	(84–97; 6)
6746 × *6750*	93	(82–100; 12)
6746 × *6754*	92	(76–99; 4)
6752 × *6746*	70	(43–99; 4)
6754 × *6454*	90	(79–97; 8)
6754 × *6750*	92	(80–100; 15)
6754 × *6755*	94	(80–98; 6)
6755 × *6743*	86	(75, 98; 2)
6755 × *6746*	95	(86–100; 5)
6762 × *6743*	96	(93–100; 6)
6762 × *6755*	97	(85–100; 11)
[Intraspecific hybridizations: *P. cistoides*]		
Dominica × Jamaica	43	(39–46; 4)
Reciprocal	48	(35–60; 6)
Dominica × Puerto Rico	46	(– ; 1)
Reciprocal	57	(40–69; 6)
Dominica × Trinidad	34	(22, 46; 2)
Reciprocal	19	(17, 21; 2)
Jamaica × Puerto Rico	96	(95, 98; 2)
Reciprocal	95	(92–97; 3)
Trinidad × Jamaica	61	(50–81; 7)
F_2	37	(1–63; 6)
Trinidad × Puerto Rico	72	(68–78; 6)
(Interspecific hybridizations)		
Trinidad × *1519*	74	(74, 75; 2)
F_2	48	(0–80; 11)
Trinidad × *6454*	68	(9–90; 22)
F_2	46	(2–81; 8)
Trinidad × *6746*	75	(60–92; 7)
Trinidad × *6755*	75	(47–86; 9)
F_2	53	(32, 74; 2)

[1] See TABLE 1 for origin and further identification of these populations. In the left-hand column the seed parent is listed first.

pollen viabilities of 13 of these progenies were above 85 percent. Two hybridizations produced progenies with average pollen viabilities below 85 percent. However, the reciprocal of one of these crosses produced progeny with a high average pollen viability. The other of the progenies involved parental taxa (vars. *caroliniana* and *glabrescens*) which produced fertile progeny when individuals from other populations were hybridized. These results indicate there are no consistent internal barriers to hybridization among the morphological variants of *P. caroliniana*, nor is sterility prevalent in the hybrid progeny.

Examination of the morphology of the F_1 hybrids in *Piriqueta caroliniana* indicates a tendency for pubescence characteristics of the more pubescent parent to be expressed in the progeny. For example, hybrids between parents with the *caroliniana* (hirsute and tomentose herbage) and *viridis* (glabrous) phenotypes resemble the *caroliniana* parent; those between *glabrescens* (tomentose pedicel and calyx only) and *viridis* phenotypes resemble the *glabrescens* parent. Those between *tomentosa* (tomentose herbage) or *caroliniana* and *glabrescens* resemble either of the first two parents. Thus, the hybrids are not intermediate between the parents in the pubescence characters which have provided the chief morphological bases for making a taxonomic distinction between them.

Ten hybrid progenies of *Piriqueta cistoides* representing six combinations of parents originating on different West Indian islands were grown (TABLE 2). Reciprocal hybrid progenies were grown for four of these hybrid combinations. With one exception, the hybrid progenies of *P. cistoides* exhibited a reduced pollen viability. The average pollen viability of the single F_2 generation was lower than that of the F_1. The pattern of low interpopulation pollen fertility in *P. cistoides* provides a sharp contrast with the pattern obtained in *P. caroliniana*.

Four progenies were obtained as a result of artificial hybridizations between plants of the Trinidad collection of *P. cistoides* and *P. caroliniana*; hybridizations using other collections of *P. cistoides* failed to produce seed. The average pollen viabilities of these interspecific hybrid progenies ranged from 68 per cent to 75 per cent (TABLE 2). A reduction in average pollen viability occurred in the three F_2 generations that were grown.

DISCUSSION

There are no consistent sterility barriers separating the morphologically distinctive variants of *Piriqueta caroliniana* in the southeastern United States that have been accorded taxonomic status by some authors. This indicates that these distinctive variants of *P. caroliniana* are very closely related genetically. The ease of making artificial hybrids among them, and the generally high fertility of the resultant F_1 hybrids and of subsequent generations, may explain in part the occurrence of natural populations which share characters of two or more of the segregate taxa, since in many areas of Florida populations of two or more of these taxa occur in close proximity. Nevertheless, the majority of herbarium specimens I

have examined at FLAS, FSU, and USF are referable to these taxa and show no obvious indication of hybridization. Some years ago Dr. J. D. Perry mapped the distribution of these variants in Florida, based on his examination of herbarium specimens at DUKE, GA, NCU, NSC, and US. Examination of his unpublished map indicates that populations of *P. caroliniana* var. *caroliniana* and var. *tomentosa* are considerably more abundant than are those of vars. *glabrescens* and *viridis*, and, furthermore, that the latter two taxa are confined to the southern half of peninsular Florida. It seems possible that field studies may reveal the existence of differences in ecological tolerances of these four taxa and that the differences may provide the basis for their continued genetic and morphological integrity over much of their ranges.

The low interpopulation crossability and the associated hybrid sterility in *Piriqueta cistoides* are unexpected in view of the contrast these results provide with the behavior of the closely related *P. caroliniana*. The degree of morphological differentiation among the plants of *P. cistoides* used in the crossing program was considerably less than that in material of *P. caroliniana*. Nevertheless, in *P. cistoides* this low degree of differentiation is in general associated with a genetic variability that results in a reduced pollen fertility of intraspecific hybrids. The high genetic individuality of each population of *P. cistoides* may be related to the autogamous breeding system and weedy habit of the species. It is probable that many of its populations are built up from one or a few initial colonizers of disturbed land. These populations are consequently rather uniform genetically. Homozygosity for random genetic changes or alterations in chromosome structure can become rapidly established in autogamous annuals, particularly under conditions where there are fluctuations in population size. In an outcrossing non-weedy perennial of stable habitats such as *P. caroliniana*, the establishment of homozygosity for such random cytogenetic changes would be a slower process, even when generation time is taken into consideration. In addition, the genetic individuality of the populations of *P. cistoides* undoubtedly is strongly reinforced by the spatial isolation of the populations on West Indian islands. This speculation suggests, therefore, that the observed differences in the fertility of interpopulation hybrids of *P. cistoides* compared with those of *P. caroliniana* is a consequence of the differences in the breeding systems, duration, population structure, and distribution patterns of these two morphologically similar species.

The close relationship between *Piriqueta cistoides* and *P. caroliniana* is indicated by their strong morphological similarity and by the moderately high fertility of their interspecific hybrids. The floral differences which separate *P. cistoides* and *P. caroliniana* are those which are associated with their different breeding systems. The showy, heterostylous flowers of *Piriqueta caroliniana* are outcrossed by halictid bees (Ornduff & Perry, 1964). In contrast, the flowers of *P. cistoides* are homostylous and are usually self-pollinated before anthesis. The smaller perianth and the reduced length of the reproductive structures of the flowers of *P. cistoides*

represent a familiar syndrome of features by which an autogamous species differs from its allogamous relatives (see Ornduff, 1969, p. 128). The floral morphology of *P. cistoides* indicates that this species has been derived from a heterostylous ancestor. The flowers of *P. cistoides* are long-homostylous, that is, they fundamentally combine a long style with the stamen length and pollen size of short-styled flowers (Ornduff, unpublished). Where heterostyly and homostyly occur in closely related taxa, homostyly is considered to be a derivative condition. Evidence from morphology, geographical distribution, and artificial hybridizations suggests that *P. caroliniana* is the probable ancestor of *P. cistoides*. The results of this study have been useful in assessing genetic relationships among populations of these two species and also in explaining some of the differences in their variation patterns. Although these results may be pertinent to the taxonomic decisions that ultimately must be made in this group, the decisions will have a stronger foundation if they include a consideration of careful field, herbarium, and nomenclatural studies.

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A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR *

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15. Lappula Gilib. Fl. Lithuan. 25. 1781.

Echinospermum Sw. ex Lehm. Asperif. 1: 113. 1818.

Type species: not indicated.

Annuals, rarely biennials or perennials. Leaves alternate. Inflorescence bracteate. Calyx divided to the base, lobes after flowering not at all to slightly enlarged. Corolla blue or white, funnelform to salverform. Faucal appendages present. Anthers included. Gynobase narrowly pyramidal. Style short, filiform; stigma capitate. Nutlets 4, attached throughout their length to the gynobase, sometimes apices free on the inner face, appendiculate, appendages glochidiate to aculeate.

About 45 species, usually distributed in temperate Europe and Asia, few in Africa, one in America.

Key to the Species

a. Nutlets smooth, tuberculate all over their surface; tubercles large, thorn-like, neither prickly nor bearing glochidia at their apices.
  b. Nutlets pyramidal to ovate-pyramidal in outline, usually longer than broad, tubercles less unequal, basal ones not much enlarged. ..... 1. *L. spinocarpos.*
  b. Nutlets broadly pyramidal in outline, usually broader than long, tubercles very unequal, basal ones much enlarged. ..... 2. *L. ceratophora.*

a. Nutlets usually rough, appendiculate at the margins, appendages bearing glochidia at their apices, usually tuberculate, on the dorsal and ventral surfaces, tubercles small, very rarely tuberculate only.
  c. Nutlets usually not, or only rarely, indistinctly margined with few glochidiate appendages; usually indistinctly verruculose, more or less smooth. ..... 3. *L. sinaica.*
  c. Nutlets distinctly margined with appendages, appendages glochidiate.
    d. Flowers and fruits sessile, fruits pyramidal, nutlets triangular, marginal appendages usually dilated at base, bases joined to form a narrow marginal wing. ..... 4. *L. sessiliflora.*
    d. Flowers and fruits with short to long pedicels, fruits ovate, nutlets ovate to oblong, marginal appendages not at all to slightly dilated at base, bases not joined to form a marginal wing.
      e. Nutlets with uniseriate marginal appendages.
        f. Inflorescence strongly elongated; nutlets small, 2–3 mm. long; marginal appendages always less than 1 mm. long; leaves linear; bracts small. ..... 5. *L. microcarpa.*

* Continued from volume 51, p. 402.

f. Inflorescence elongate to more or less contracted; nutlets usually large, 3–4(–5) mm. long; marginal appendages always longer than 1 mm., usually 1.5–2 mm. long; leaves lanceolate; bracts usually large.
g. Leaves on the lower surface subglabrous. ..... 6. *L. semiglabra.*
g. Leaves on the lower surface densely pubescent. ..... 7. *L. patula.*

e. Nutlets with multiseriate marginal appendages.
h. Nutlets with three series of appendages. .. 8. *L. consanguinea.*
h. Nutlets with two series of appendages.
i. Corolla funnelform to salverform, 3.5–7 mm. in diameter; stem covered with soft, white, appressed trichomes. ..... 9. *L. barbata.*
i. Corolla salverform, 3–4 mm. in diameter; stem covered with stiff, spreading trichomes.
j. Appendages of the inner series much longer than those of the outer series. ..... 10. *L. heteracantha.*
j. Appendages of the inner series more or less equalling those of the outer series. ..... 11. *L. myosotis.*

1. **L. spinocarpos** (Forssk.) Ascherson & O. Kuntze, Acta Horti Petrop. **10**: 215. 1887; Riedl in Rechinger, Fl. Iranica **48**: 69. 1967.

Anchusa spinocarpos Forssk. Fl. Aegypt.-Arab. 41. 1775.
Echinospermum vahlianum Lehm. Asperif. **1**: 132. 1818.
E. tuberculosum Ledeb. in Eichw. Pl. Casp.-Cauc. **2**: 11. 1831.
E. spinocarpos (Forssk.) Boiss. Fl. Orient. **4**: 249. 1875.
Sclerocaryopsis spinocarpos (Forssk.) Brand, Pflanzenr. IV. **252** (Heft 97): 98. 1931.

TYPE: Alexandria, *Forsskål, s. n.* (C).

ICON.: Brand l.c. *fig. 1 B.* 1931, under *Sclerocaryopsis spinocarpos.*

Annual herb, usually decumbent or sometimes erect, branched at the base, 5–20 cm. tall. Stem and branches covered densely with appressed to subappressed white trichomes, arising from tiny bulbous bases. Basal leaves usually linear-spathulate, entire, obtuse, 15–35 mm. long, 1–3 mm. broad, covered densely on both surfaces with white subappressed trichomes; cauline leaves shorter and narrower, sometimes narrowly lanceolate, not much attenuated towards the base. Inflorescence lax, bracteate; pedicels in flower about 1 mm. long, in fruit elongated to 4 mm. Calyx divided to the base, lobes in flower 1–2 mm. long, to 0.75 mm. broad, erect, covered with white appressed trichomes, in fruit enlarged, to 7 mm. long and 1.5 mm. broad, with subpatent trichomes arising from prominent tuberculate bases. Corolla infundibuliform, 3–4 mm. long, tube white, limb blue, more or less campanulate. Nutlets pyramidal to ovate-pyramidal, usually longer than broad, 3–5 mm. long, tuberculate, tubercles large, thorn-like, not prickly, very rarely glochidiate, less unequal, basal ones not much enlarged, surface smooth to verruculose or rarely minutely aculeate-tuberculate.

DISTRIBUTION: North Africa, Sinai, Palestine, Iraq, Iran, Afghanistan, central Asia, Tien Shan, Pamir Alaj, West Pakistan.

West Pakistan: DERA GAZI KHAN DIST.: Fort Munro, 1800 m., *Kazmi 1862a* (PES); *Rechinger 29727* (W). QUETTA DIST.: 45 miles from Sibi to Quetta in Bolan Pass, *Kazmi 1398b* (PES); ZHOB DIST.: between Zhob and Sambaza, 1500 m. *Kazmi 1923b* (PES); *Rechinger 29845* (W); 30 km. N. Fort Sandeman, *Rechinger 29858* (W). Reported from: Sibi, *Banerji* in *Williams 55*; Nai Ublo, *Harsukh 20603*.

The leaves of *Lappula spinocarpos* vary from linear to linear-spathulate, to narrowly lanceolate, or sometimes to oblong-ovate. The surface of the nutlets and of the large tubercles varies from shining and smooth to rough, to minutely verruculose, or even to minutely aculeate. Similarly the trichomes on the leaves are very dense and appressed in some cases (Persia, May, 1869, Bunge (GH)), while loose and erect in others (specimens from Kasakistan, Caucasus, Egypt, and Iraq).

2. **L. ceratophora** (M. Pop.) M. Pop. Fl. URSS **19**: 417. 1953; Riedl in Rechinger, Fl. Iranica **48**: 70. 1967.

Echinospermum ceratophorum M. Pop. in Korov. Kultiasow Pop. Descr. Pl. Nov. Turk. 67. *t. 17*. 1916.

TYPE: In provincii bucharicis Karschi et Burdalyk Turkestaniae, *I. I. Sprygin & M. V. Kultiasow s. n.* (LE).

ICON.: M. Pop. l. c. 67. *t. 17*. 1916; M. Pop. l. c. *t. 20, fig. 1*. 1953.

Annual, usually decumbent sometimes erect, to 15 cm. tall, much branched at the base. Stem and branches densely covered with white, short, depressed trichomes. Leaves linear to linear-spathulate, obtuse, entire, 20–40 mm. long, 1–3 mm. broad, both surfaces covered with white appressed to subappressed short trichomes, margins (especially towards the base) bearing some scattered long trichomes. Inflorescence lax, bracteate; pedicels in flower up to 1 mm. long, in fruit elongated to 4 mm. Calyx divided to the base, lobes in flower 1–2 mm. long and 0.75 mm. broad, erect, in fruit enlarged to 3–6 mm. long and 1.5 mm. broad, erect or slightly curved towards the fruit, covered densely with subappressed trichomes, arising from prominent tuberculate bases. Corolla blue with a white eye, infundibuliform, slightly dilated at the throat, lobes erect or patent. Nutlet broadly pyramidal, usually broader than its length, tuberculate, tubercles large, thorn-like, usually smooth and shining at the surface, rarely rough, very unequal, basal ones much enlarged, to 2 mm. long.

DISTRIBUTION: Iran, Afghanistan, West Pakistan, Syr-Darya, Amu Darya, Kara Kum, Pamir Alaj.

West Pakistan: QUETTA DIST.: Quetta to Chaman, 30 km. northeast of Quetta, *Kazmi 1468b* (PES); *Lamond 958* (E); *Rechinger 28866, 28908b* (W).

The only difference between *Lappula spinocarpos* and *L. ceratophora*

is in the form of the fruit and the length of the tubercles. In *L. spinocarpos* the nutlets are longer than broad with comparatively shorter tubercles, varying in length from the top to the base of the nutlet. Usually the middle ones are the longest, but this character is not very constant and sometimes the lower tubercles are longer than the middle ones, thus bringing this species very close to *L. ceratophora* in this respect. In *L. ceratophora* the nutlets are broader than long with comparatively longer tubercles, increasing in their length, more or less gradually, from the top towards the base, the basal tubercles are the longest. This character is more stable in *L. ceratophora*. For distinguishing the two species from one another it is necessary to consider and correlate the ratio of the length and breadth of the nutlets and the length ratio of the tubercles from the top to the base of the nutlets. There is little difference in the form of leaves or floral parts in the two species. After examination of more material *L. ceratophora* may prove to be a subspecies or variety of *L. spinocarpos*.

3. **L. sinaica** (DC.) Ascherson ex Schweinf. Mem. Inst. Egypt **2**: 111. 1887; Brand, Pflanzenr. IV. 252(Heft 97): 144. 1931; M. Pop. Fl. URSS **19**: 475. 1953; Riedl in Rechinger, Fl. Iranica **48**: 76. 1967.

Echinospermum sinaicum DC. Prodr. **10**: 141. 1846; Boiss. Fl. Orient. **4**: 251. 1875.

E. kotschyi Boiss. Diagn. Pl. Orient. **7**: 29. 1846.

E. divaricatum Bunge, Reliq. Lehm. 410. 1851 *ex descr.*; Mem. Acad. Sci. St. Pétersb. **7**: 410. 1851.

Lappula divaricata B. Fedtsch. Rast. Turk. 663. 1915.

TYPE: Sinai, *Aucher 118* (G).

Annual erect to more or less decumbent, less branched herb, 6–50 cm. tall. Stem and branches flexuose, slender, covered with white, appressed to subpatent trichomes arising from minute white tuberculate bases. Basal leaves petiolate, oblong to elliptic-oblong, entire, obtuse, (including petioles) 15–50 mm. long, 5–15 mm. broad, covered on both surfaces loosely to densely with equal to unequal long, subappressed trichomes in the old leaves sometimes arising from white tuberculate bases; cauline leaves sessile, gradually decreasing in size upwards. Inflorescence in flower long, very much elongated in fruit; pedicels lacking to very short in flower, elongated to 5 mm. and reflexed in fruit. Calyx divided to the base, lobes linear-oblong in flower, 1–1.5(–2) mm. long, hairy, erect, not much enlarged in fruit. Corolla bluish-purple with a white or yellowish eye, infundibuliform, ± 3 mm. long, ± 2.5 mm. in diameter; faucal appendages trapeziform. Nutlets oblong-ovoid, 2–2.5 mm. long, indistinctly margined, tuberculate to quite smooth, sometimes indistinctly verruculose or bearing few short glochidiate appendages, totally attached to the gynobase.

DISTRIBUTION: Sinai, Iraq, Iran, Caucasus, Afghanistan, Turkestan, Pamir Alaj, Tien Shan, West Pakistan, northwest India.

West Pakistan: CHITRAL STATE: Chitral village, 2 miles south, on gravel slope, 1500 m., *Stainton 2213* (BM). KALAT STATE: between Kalat and Mastung, 40 km. from Kalat, 2000 m., *Kazmi 1278b* (PES); *Rechinger 28377* (W). QUETTA DIST.: Quetta, *Lace s. n.* (E); Spin Karez, 1900 m., *Kazmi 1632c* (PES); *Rechinger 29235* (W); between Qila Abdullah and Sheila Bagh, 2300 m., *Kazmi 1529* (GH, PES); Bolan Pass, 2000 m., *Kazmi 1407b* (PES); *Rechinger 28423* (W); between Kolpur and Machh, 900 m., *Kazmi 1401b* (PES); *Rechinger 28431* (W). Reported from Baluchistan: Khojak, 2300 m., *Rechinger 29067* (W); Inter Bostan et Saran Tangai, 1800 m., *Rechinger 29192* (W); Ziarat, 2100 m., *Rechinger 29361* (W); Tak, 30 km. S. Quetta, 2100 m., *Rechinger 28395* (W); 10 miles S. Kalat, 1900–2200 m., *Rechinger 28362* (W).

4. **L. sessiliflora** (Boiss.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 107. 1893; Brand, Pflanzenr. IV. 252 (Heft 97): 144. 1931; M. Pop. Fl. URSS 19: 477. 1953; Riedl in Rechinger, Fl. Iranica 48: 78. 1967.

Echinospermum sessiliflorum Boiss. Diagn. Pl. Orient. **11:** 124. 1849; Fl. Orient. **4:** 253. 1875.
Heterocaryum divaricatum Stocks ex Boiss. Fl. Orient. **4:** 253. 1875.
Cynoglossospermum sessiliflorum O. Kuntze, Rev. Gen. Pl. **2:** 437. 1891.

TYPE: Persia: Esfahan, *Aucher 5017* (G).

ICON.: Brand, l. c. *fig. 15. F–J.* 1931.

Annual, erect or decumbent herb, branched at the base, 5–20(–25) cm. tall. Branches divaricate, curved. Stem and branches densely covered with short, white to brownish, appressed trichomes. Basal leaves petiolate, linear-oblong to oblong-spathulate, entire, obtuse, (including petioles) 15–25 mm. long, 1–2.5 mm. broad, covered on both surfaces uniformly with thin, patent, white trichomes to 0.5 mm. long, intermixed with scattered thick trichomes, to 1 mm. long, arising from white tuberculate bases; cauline leaves sessile, narrower and shorter, covered uniformly with trichomes 0.5–0.75 mm. long, arising from prominent, white, tuberculate bases. Inflorescence long, bearing distant sessile flowers or fruits, bracteate, bracts leaflike, oblong to oblong-ovate. Calyx divided to the base, lobes oblong, hairy, erect, not enlarged in fruit, to 2 mm. long. Corolla blue, infundibuliform-campanulate, 2–2.5 mm. long; faucal appendages minute to inconspicuous. Nutlets broadly triangular, 2.5–3 mm. long, margined with uniseriate appendages, appendages glochidiate at their apex, free to confluent at base, sometimes forming quite broad scarious wings at margins, dorsal and ventral surfaces tuberculate to tuberculate-verruculose, rough, totally attached to the gynobase.

DISTRIBUTION: Iraq, Iran, Caucasus, Pamir Alaj, Tien shan, Turkestan, Afghanistan, West Pakistan.

West Pakistan: KALAT STATE: Between Kalat and Mastung, 2000 m., *Kazmi 1273* (PES); *Rechinger 28386* (W). QUETTA DIST.: West of Ziarat, 2200 m., *Kazmi 1669b* (PES); *Rechinger 29285* (W); Spin Karez 1900 m., *Kazmi 1641b* (PES); *Rechinger 29234* (W); between Quetta and Ziarat, *Kazmi 1574b* (PES);

near Kolepur, *Kazmi 1400b* (PES). Reported from: Quetta, inter Qila Abdullah et Sheila Bagh, 1600–1900 m., *Rechinger 29011* (W); inter Dulai et Kanak, 1600 m., *Rechinger 29095* (W). Baluchistan, *Stocks s. n.* (GH-type of *Heterocaryum divaricatum* Stocks ex Boiss.).

The sessile fruits and triangular nutlets of *Lappula sessiliflora* distinguish this species from allied species having nutlets with appendaged margins. The appendages on the margins of the nutlets of *L. sessiliflora* are very variable in length and breadth. Sometimes they are quite distant to slightly confluent at their bases, while in other cases they are so strongly joined together that they form a broad scarious wing at the margins. These wings may be turned vertically to give the nutlets a cup-like appearance. Usually narrowly winged and broadly winged nutlets are found on the same plant at different stages of development.

5. **L. microcarpa** (Ledeb.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 107. 1893; Brand, Pflanzenr. IV. 252(Heft 97): 142. 1931, excl. syn. *E. rigidum* DC. [ex Persia]; M. Pop. Fl. URSS **19**: 462. 1953; Riedl in Rechinger, Fl. Iranica **48**: 74. 1967.

Echinospermum microcarpum Ledeb. Fl. Alt. **1**: 202. 1829; Icon. Fl. Rossica **2**: *t. 183*. 1830; DC. Prodr. **10**: 140. 1846; Boiss. Fl. Orient. **4**: 251. 1875.
E. stylosum Kar. & Kir. Bull. Soc. Nat. Moscou **14**: 715. 1841; DC. Prodr. **10**: 140. 1846.
E. oligacanthum Ledeb. Fl. Rossica **3**: 161. 1846–1851.
Heterocaryum inconstans Vatke, Zeitschr. Ges. Naturw. **11**: 129. 1875.

TYPE: Habitat in lapidosis montium Arkaul, versus cacumen, in montibus ad rivulum Urmuchaika prope Buchtarminsk, *Ledebour s. n.* (LE ?).

ICON.: Brand, l. c. *fig. 15. A–E.* 1931; Ledeb. l. c. *t. 183.* 1830, under *Echinospermum microcarpum.*

Annual or biennial, erect herb, 15–55 cm. tall. Stem solitary or many, simple or usually branched above, branches long, divaricate; stem and branches covered with white, appressed trichomes, 0.5–0.75(–1) mm. long on the lower part of the stem, usually intermixed with longer and stouter trichomes arising from prominent, white, tuberculate bases. Basal leaves oblong, obtuse, gradually attenuated towards the base, 30–45 mm. long, 2–3 mm. broad, forming a rosette, covered densely or loosely on both surfaces with spreading trichomes to 2 mm. long, arising from prominent white tuberculate bases; cauline leaves sessile, linear-oblong, narrower and shorter. Inflorescence short, bearing closely set, subsessile flowers, later much elongated, with pedicellate fruits up to 5 mm. apart; pedicels hairy, stout, erect, to 2 mm. long; bracts small. Calyx divided to the base, lobes 1–2 mm. long, erect, not much enlarged in fruit. Corolla bluish-white, infundibuliform, 2.5–3 mm. long, 2–3 mm. in diameter; faucal appendages 0.5–0.75 mm. long. Nutlets ovoid, 2.5–3 mm. long, with a single series of short, not glochidiate appendages at the margin (not more than 1 mm. long), dorsal and ventral surface tuberculate or granulate.

DISTRIBUTION: Iran, Caspian Arals, Turkestan, Tien shan, Pamir Alaj, Afghanistan, West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Agram, Arkari Gol. west of Tirich Mir, 3000 m., *Stainton 2616* (BM); Kafiristan, Rumbur, hillside facing south, 2400 m., *Bowes Lyon 675* (BM). GILGIT AGENCY: Baltistan, Kasurmik to Doghani, 2500 m., *R. R. Stewart 20799* (GH). KALAT STATE: near Mastung, *Kazmi 1324c* (PES). QUETTA DIST.: Quetta, *Kazmi s. n.* (PES); West of Ziarat, 2400 m., *Kazmi 1654b* (PES); Ziarat, 2400 m., *Jafri & Akbar 2071* (BM); between Hindu Bagh and Quetta, *Jafri & Akbar 2357* (BM).

Kashmir: LADAK: Bod Kharbu, *Koelz 6239* (GH, US).

6. **L. semiglabra** (Ledeb.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. **3a**: 104. 1893; M. Pop. Fl. URSS **19**: 430. 1953; Riedl in Rechinger, Fl. Iranica **48**: 75. 1967.

Echinospermum semiglabrum (Ledeb.) Fl. Alt. **1**: 204. 1829; Icon. Fl. Rossica **1**: *t. 28.* 1829; Fl. Rossica **3**: 158. 1847; DC. Prodr. **10**: 138. 1846; Boiss. Fl. Orient. **4**: 251. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 163. 1883.

Lappula redowskii (Hornem.) Greene var. *patula* (Lehm.) Nels. & Macbr. subvar. *semiglabra* (Ledeb.) Brand, Pflanzenr. IV. **252** (Heft 97): 149. 1931.

Echinospermum caspicum Fisch. & C. A. Mey. Index Sem. Hort. Petrop. **5**: 34. 1838; DC. Prodr. **10**: 138. 1846.

TYPE: Habitat in sabulosis ad fl. Irtysch, *Ledebour s. n.* (LE).

ICON.: Ledeb. l. c. **1**: *t. 28.* 1829; M. Pop. l. c. **19**: *t. 21. fig. 2.* 1953.

Annual, erect herb, 15–50 cm. tall. Stem simple or branched above; stem and branches covered with short, appressed white trichomes. Basal leaves petiolate, oblong-spathulate, obtuse, entire, (including petioles) 40–50 (–60) mm. long, 6–9 mm. broad, upper surface usually glabrous or sometimes with few scattered trichomes, lower surface usually loosely, sometimes, especially in the old leaves, densely covered with white, spreading trichomes to 1 mm. long, arising from prominent white tuberculate bases; cauline leaves gradually decreasing in size upwards, sessile, more or less lanceolate, acutish. Inflorescence short in flower, much elongated later in fruit, flexuose, bracteate, bracts small. Flowers subsessile, fruits pedicellate; pedicels hairy, erect, to 3 mm. long. Calyx divided to the base, lobes oblong, hairy, erect, 1–1.5 mm. long in flower, enlarged in fruit to 3 mm. long, ± 0.5 mm. broad. Corolla bluish-white to light blue, campanulate, 3–3.5 mm. long, 3–4 mm. in diameter; faucal appendages trapeziform. Nutlets narrowly ovoid 4–5 mm. long, margined with uniseriate glochidiate appendages 2–3 mm. long, slightly dilated at base, dorsal middle area carinate, usually aculeate, outer surface slightly tuberculate.

DISTRIBUTION: URSS, Afghanistan, West Pakistan, Kashmir, northwest India.

West Pakistan: GILGIT AGENCY: Baltistan, Thalle La, 2200 m., *R. R. Stewart 20584a* (GH); rocky barren slopes near south end of Satpura Lake, ca. 4.5 miles south of Skardu, 3000 m., *Webster & Nasir* (GH), Satpura Nullah, above Skardu, 2700 m., *R. R. Stewart 20368* (GH). MAKRAN DIST.: between Hushab and Panjgur, 20–30 km. from Panjgur, *Kazmi 1190b* (PES); *Lamond 567* (E). 20 miles from Panjgur towards Nag, *Kazmi 1243c* (PES). ZHOB DIST.: Shingarh, 50 km. north of Fort Sandeman, 2000 m., *Rechinger 29894* (W); *Harsukh 20595* (K). Reported from: Kharan and Quetta *Haughes Buller 23159*.

Kashmir: Miscellaneous: Hab. Tibet Occ. regio temp. 10,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson 10* (GH); 11,000–12,000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

7. **L. patula** (Lehm.) Ascherson ex Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. **3a**: 107. 1893; M. Pop. Fl. URSS. **19**: 436. 1953. Riedl in Rechinger, Fl. Iranica **48**: 76. 1967.

Echinospermum patulum Lehm. Asperif. 124. 1818; Ledeb. Fl. Alt. **1**: 200. 1829; DC. Prodr. **10**: 137. 1846; Boiss. Fl. Orient. **4**: 250. 1875.
Lappula redowskii (Hornem.) Greene var. *patula* (Lehm.) Nels. & Macbr. Bot. Gaz. **61**: 39. 1916; I. M. Johnston, Contr. Gray Herb. **70**: 49. 1924.

TYPE: In deserto Caucasico-Caspico, ad Kuman et Terek nec ad Wolgam inferiorem area Sareptanam colonium et urbem Astrachan, *Lehmann s. n.* (HBG).

ICON.: Hegi, Ill. Fl. Mitt.-Eur. **5**: 3. *fig. 3098a*. 1927.

Annual, branched near the base, to 50 cm. tall; branches long-divaricate. Stem and branches covered with short appressed white trichomes. Basal leaves linear-oblong to linear-spathulate, gradually attenuated towards the base, obtuse, entire, 40–60 mm. long, 6–9 mm. broad, covered on both surfaces, usually densely, (sometimes loosely) with short, white, appressed trichomes, intermixed, more or less, with longer ones, arising from white tuberculate bases; cauline leaves gradually reduced in size upwards. Inflorescence short in flower, later much elongated, lax, bracteate, bracts small, leaflike. Flowers subsessile to short pedicellate; pedicels erect, hairy, to 1.5 mm. long in flower, elongated to 2.5 mm. in fruit. Calyx divided to the base, lobes linear to oblong, 1–2 mm. long in flower, much enlarged to 5 mm. long in fruit. Corolla bluish-white to blue, campanulate, 3–3.5 mm. long, 3–4 mm. diameter; faucal appendages trapeziform, prominent. Nutlets ovoid, 3–4 mm. long, margined with uniseriate appendages, appendages 1.5–3 mm. long, glochidiate at apex, dorsal middle area tuberculate, rarely aculeate, externally slightly tuberculate.

DISTRIBUTION: URSS, Iran, Afghanistan, West Pakistan, Kashmir, northwest India, China.

Kashmir: LADAK: Tsaka La, 5000 m., *Koelz 2368* (GH); Kharbu to Dras, 3000 m., *R. R. Stewart 2115* (GH). Miscellaneous: Hab. Tibet Occ. regio temp., 12,000–14,000 ped., Herb. Ind. Or. Hook. f. & Thoms. Herb. no. *2496849*, *2500079* (US); *s.n.* (GH).

Only two collections of *Lappula patula* have been made from Kashmir, but the species is to be expected throughout the northern parts of Kashmir and West Pakistan. *Lappula patula* is very closely related to *L. semiglabra* from which it may be distinguished by its habit of branching near the base, by its leaves densely hairy on both surfaces, and by its smaller and broader nutlets. In *L. semiglabra* the stems are branched in the upper part, the leaves are usually glabrous on the upper surface, and the nutlets are narrowly ovoid, 4–5 mm. long, margined with appendages 2–3 mm. long.

8. **L. consanguinea** (Fisch. & C. A. Mey.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 107. 1893; M. Pop. Fl. URSS 19: 447. 1953.

Echinospermum consanguineum Fisch. & C. A. Mey. Index Sem. Hort. Petrop. **5**: 35. 1838; DC. Prodr. **10**: 137. 1846; Ledeb. Fl. Ross. **3**: 157. 1847.

E. lappula var. *consanguineum* (Fisch. & C. A. Mey.) Regel, Bull. Soc. Nat. Moscou **41**(1): 89. 1868.

Cynoglossospermum consanguineum O. Kuntze, Rev. Gen. Pl. **2**: 438. 1891.

Lappula echinata var. *consanguinea* (Fisch. & C. A. Mey.) Brand, Pflanzenr. IV. **252**(Heft 97): 140. 1931.

TYPE: Hab. in regionibus altaicus, *Bunge s. n.* (LE).

ICON.: M. Pop. l. c. *t. 22. fig. 9.* 1953.

Annual or biennial, erect, up to 50 cm. tall, usually branched above, branches flexuose, to 25 cm. long. Stem and branches covered with unequal, subappressed to patent trichomes to 1.5 mm. long. Basal leaves oblong-lanceolate, entire, obtuse, narrowed towards the base, to 7 cm. long, 11 mm. broad, nerves sunken on the upper surface, prominent below, both surfaces covered with scattered, white, spreading trichomes, to 1 mm. long, arising from prominent tuberculate bases; cauline leaves lanceolate, acutish, gradually reduced in size upwards. Inflorescence lax, short, elongated in fruit, bracteate. Flowers subsessile to very short pedicellate, pedicels of old fruits pubescent, erect, to 2 mm. long. Calyx divided to the base, lobes linear-oblong, in flower up to 2 mm. long, 0.5 mm. broad, in fruit slightly enlarged, to 3 mm. long and 0.7 mm. broad. Corolla blue with a white eye, infundibuliform, 2.5–3 mm. long; faucal appendages prominent. Nutlets ovate, 2–2.5 mm. long, 1–1.5 mm. broad at the base, margined with three series of appendages, appendages glochidiate at apex, slightly dilated at base, rarely confluent to form a wing, appendages of the inner series longest, to 1.5 mm. long; dorsal middle area tuberculate.

DISTRIBUTION: Turkestan, Altai, West Pakistan, Kashmir.

West Pakistan: GILGIT AGENCY: Lower Rupal Nullah, Nanga Parbat, 2700 m., *R. R. Stewart 18862* (GH).

The three series of appendages at the margin of the nutlets distinguish *Lappula consanguinea* from the closely related species *L. barbata*, which

has two series of appendages on its nutlets. Sometimes the appendages of the outermost series are very short, but they are always conspicuous. The specimen cited above is identical to the specimens collected from Altai and Turkestan. Brand (*l. c.* 1931) gives the distribution of *L. consanguinea* as extending to Eastern Europe, but I did not find any specimen from that area in the European collections.

9. **L. barbata** (M. Bieb.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. **3a**: 107. 1893; Brand, Pflanzenr. IV. **252** (Heft 97): 140. 1931 excl. var. *arragonensis*; M. Pop. Fl. URSS. **19**: 461. 1953; Riedl in Rechinger, Fl. Iranica **48**: 72. 1967.

Myosotis barbata M. Bieb. Fl. Taur.-Cauc. **1**: 121. 1808.
Echinospermum barbatum Lehm. Asperif. **1**: 128. 1818; DC. Prodr. **10**: 137. 1846; Ledeb. Fl. Rossica **3**: 156. 1847; Boiss. Fl. Orient. **4**: 250. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 163. 1883.
Myosotis saxatilis Pall. Nova Act. Petrop. 306. 1792, *nomen nudum*.
Echinospermum filiforme Godet in DC. Prodr. **10**: 140. 1846.
Lappula saxatilis (Pall.) Kusn. Mat. Fl. Kauk. **4**(2): 183. 1930.

TYPE: Habitat in Tauriae montibus calcareis circa Karassubasar et ad Caucasum, without citation of collector's name, *s. n.* (LE).

ICON.: M. Bieb. Cent. Pl. Rar. *t. 36*. 1810.

Erect annual or biennial, to 65 cm. tall. Stem simple to branched, branches sometimes divaricate; stem and branches covered with white, soft, appressed to subappressed trichomes. Basal leaves numerous, forming a compressed rosette, lanceolate to linear-lanceolate, entire, obtuse to acutish, gradually tapering towards the base, to 7 mm. long and 10 mm. broad, covered on both surfaces with short appressed to subpatent white trichomes, arising from white tuberculate bases; cauline leaves sessile, linear, to 3 mm. broad, in length gradually reduced upwards. Inflorescence axillary or terminal, short in flower, later much elongated. Flowers bracteate, subsessile to short pedicellate; pedicels hairy, erect to 1.5(–2) mm. long in fruit. Calyx divided to the base, lobes linear-oblong, erect, hairy, 2.5–3 mm. long in flower, enlarged to 5 mm. long in fruit. Corolla white to light blue with a white or yellow eye, infundibuliform-campanulate, 3.5–7 mm. in diameter, faucal appendages oblong. Nutlets 3–4 mm. long, margined with two series of appendages, appendages glochidiate at apex; middle area tuberculate or rarely aculeate.

Lappula barbata is variable in the size of flower and the length of the marginal appendages of the nutlets. Two varieties may be distinguished.

9a. Var. **barbata**

Corolla 5–7 mm. in diameter; marginal appendages of the nutlets more or less equal in length.

DISTRIBUTION OF VAR: Turkey, Caucasus, Turkestan, Iraq, Iran, Afghanistan.

9b. Var. **cariensis** (Boiss.) Brand, Pflanzenr. IV. 252 (Heft 97): 141. 1931; Riedl in Rechinger, Fl. Iranica **48**: 72. 1967.

Echinospermum cariensis Boiss. Diagn. Pl. Orient. **4**: 40. 1844; DC. Prodr. **10**: 141. 1846.
Echinospermum barbatum (M. Bieb.) Lehm. var. *cariensis* (Boiss.) Boiss. Fl. Orient. **4**: 250. 1875.
Lappula echinata Gilib. var. *cariensis* O. Kuntze, Acta Horti Petrop. **10**: 214. 1887.

TYPE: Hab. Anatolia, in collibus argillosis ad meridiam Cadmi et ad orientem urbis Danisleh, without citation of collector's name, *s. n.* (G).

Corolla 3.5–5 mm. in diameter, marginal appendages of the outer series of nutlets much shorter than those of the inner series.

DISTRIBUTION: Turkey, Syria, Armenia, Iraq, Iran, USSR, Afghanistan, West Pakistan, Kashmir, northwest India.

West Pakistan: CHITRAL STATE: Barum Gol, above Shokor Shal, 3600 m., *Wendelbo s.n.* (BERG). QUETTA DIST.: Urak near Quetta, 1800 m., *R. R. Stewart 602b* (MICH.); near Ziarat, 2500 m., *Kazmi 1672b* (PES), *Rechinger 29392* (W), *Fernandes 6269* (GH); Ziarat, Zarghun, *Santapau 6419* (GH). WAZIRISTAN AGENCY: Razani, 2500 m., *Lester Garland s.n.* (E). Miscellaneous: Scind, *Stocks s.n.* (GH); Baluchistan, *Elliott s.n.* (K).
Kashmir: Mitsahoi on Ladak Road, 3300 m., *R. R. Stewart 9993* (GH); Zaskar, Lagong, 4000 m., *Koelz 5408* (GH, US); Kargia, 4000 m., *Koelz 5454* (GH, US).

10. **L. heteracantha** (Ledeb.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. IV. 3a: 107. 1897; M. Pop. Fl. URSS **19**: 427. 1953; Riedl. in Rechinger, Fl. Iranica **48**: 72. 1967.

Echinospermum heteracanthum Ledeb. Suppl. Index Sem. Hort. Dorpat. 3. 1823; Fl. Rossica **3**: 157. 1847; DC. Prodr. **10**: 137. 1846; Boiss. Fl. Orient. **4**: 249. 1875.
Lappula echinata Gilib. var. *heteracantha* (Ledeb.) O. Kuntze in Acta Horti Petrop. **10**: 214. 1887; Brand, Pflanzenr. IV. **252** (Heft 97): 139. 1931, *pro parte*.
Echinospermum semicinctum Stev. Bull. Soc. Nat. Moscou **24**: 605. 1851.

TYPE: Habitat in Astrachan, cultivated from the seed collected from Astrachan, without citation of collector's name.

ICON.: Ledeb. in Eichw. Pl. Casp.-Cauc. *t. 21.* 1831–1833.

Annual or biennial herb, to 50 cm. tall. Stems solitary to many, simple to branched, branches long, divaricate; stem and branches covered with stiff, short or long, usually spreading sometimes subappressed, grayish or white trichomes arising from prominent tuberculate bases; trichomes on

the lower part of the stem falling off with age. Basal leaves usually forming rosettes, oblong, gradually narrowed towards the base, entire, obtuse, 2–7 cm. long, 3–8(–12) mm. broad, covered on both surfaces with stiff, short or long, patent or subpatent grayish trichomes arising from tuberculate bases; cauline leaves gradually reduced in size upwards; upper leaves sessile, broader than the lower ones, acutish. Inflorescence lax, bracteate, much elongated in fruit. Flowers subsessile to short pedicellate; pedicels much elongated in fruit, to 3 mm. long, pubescent, erect, tapering towards the base. Calyx divided to the base, lobes in flower erect, 1.5–2 mm. long, in fruit spreading, to 3.5 mm. long. Corolla light blue with a white or yellowish eye, salverform, 3–4 mm. long, limbs 3–4 mm. diameter; faucal appendages oblong, conspicuous. Nutlets 2–3 mm. long, margined with two series of appendages, appendages glochidiate at their apices, appendages of the outer series much shorter than those of the inner series; middle dorsal and ventral surfaces tuberculate to minutely aculeate.

DISTRIBUTION: Eastern Europe, Iran, USSR, Central Asia, West Pakistan, Kashmir, northwest India.

West Pakistan: GILGIT AGENCY: Nomal, 1700 m., *R. R. Stewart 26337* (BM); Naltar, 3000 m., *R. R. Stewart 26338* (BM); Astor valley, 2700–3000 m., *R. R. Stewart 22024* (GH); near Chorit, Rupal Nullah, 2700 m., *R. R. Stewart 22844* (GH, US); Baltistan, Chatpani Nulla, 3500 m., *Duthie 13859* (K). Miscellaneous: Baluchistan: Sinkachh, *Harsukh 20594* (K).

Kashmir: Zoji Pass, 3300 m., *R. R. Stewart 21199a* (GH), *21247* (GH, US); Zoji Pass to Matayan, 3300 m., *R. R. Stewart 7403* (K); Dras to Tibet, 3000 m., *Gammie* (3. 8. 1891) *s.n.* (K); Dras to Mistahoi, Ladak Road, *R. R. Stewart 22340* (GH); Shingo valley near Gulteri, *R. R. Stewart 22231b* (GH). Miscellaneous: Hab. Tibet Occ. Regio temp., 12000–14000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH).

11. **L. myosotis** Moench, Meth. 417. 1794; Riedl in Rechinger, Fl. Iranica **48**: 71. 1967.

Myosotis lappula L. Sp. Pl. 131. 1753.
Lappula echinata Gilib. Fl. Lithuan. 25. 1781, *nomen illegitimum*.
Echinospermum squarrosum Reichenb. Fl. Germ. Excurs. 345. 1834.
Echinospermum ispahanicum Boiss. Diagn. Pl. Orient. **11**: 123. 1849.
E. lappula (L.) Lehm. Asperif. **1**: 121. 1881.
Lappula echinata Gilib. var. *eu-echinata* Brand, Pflanzenr. IV. **252** (Heft 97): 138. 1931.

TYPE: Habitat in Europae argillosis nudis, ruderatis Herb. No. 180.9 (LINN).

ICON.: Reichenb. Icon. Fl. Germ. **18**: *t. 128. fig. 2* and *7–19*. 1858.

Erect annual or biennial herb. Stems solitary or many, usually simple, sometimes branched above; stem and branches covered with short, white trichomes, arising from tuberculate bases. Basal leaves oblong-spathulate, entire, obtuse, gradually or abruptly attenuated into a long petiole, to 7

cm. long and 3–12 mm. broad, covered on both surfaces, loosely or densely, with thin, long, white trichomes, arising from white tuberculate bases; cauline leaves shorter, narrower, acutish. Inflorescence short in flower, later, in fruit, elongated, lax and bracteate. Flowers short pedicellate; pedicels elongated in fruit to 3 mm., erect, hairy. Calyx divided to the base, lobes linear, acutish, hairy, in flower 2–3 mm. long, in fruit narrow-lanceolate, to 4–5 mm. long and 1 mm. broad, spreading to sometimes reflexed. Corolla blue, salverform, ca. 4 mm. long, limbs 3–4 mm. in diameter; faucal appendages oblong. Nutlets 2.5–3 mm. long, margined with two series of appendages, appendages of both series more or less equal in length, glochidiate at apex, middle dorsal area verruculose-granulate, externally more or less tuberculate.

DISTRIBUTION: Central and Eastern Europe, Caucasus, Siberia, Aral-Caspian, Dsungare-Tarbagatai, Persia, Afghanistan, West Pakistan, North America.

West Pakistan: KURRAM AGENCY: Kurram Valley, *Aitchison 198* (GH); Reported from: Quetta Dist.: Ziarat, *R. R. Stewart 600*; Urak, *Crookshank 104*; Zarghun, *Crookshank 368, 384.*

The closest relative of *Lappula myosotis* is *L. heteracantha*, from which it may be easily distinguished by the appendages at the margins of the nutlets being essentially equal in length in both series.

16. **Lepechiniella** M. Pop. Fl. URSS 19: 713. 1953.

TYPE SPECIES: *L. transalaica* (B. Fedtsch.) M. Pop. (lectotype species).

Annual or perennial herbs. Calyx divided nearly to the base; lobes 5, various, not at all to slightly enlarged in fruit. Corolla white or blue, tubular-infundibuliform, tube short, limbs patent; faucal appendages developed. Stamens included, below the faucal appendages. Gynobase narrowly prismatic, tetragonous. Nutlets appendiculate, at the margins appendages free at base or confluent and forming a marginal wing; nutlets ventrally keeled above the minute sub-basal, areola, attached to the gynobase, free at apex. Style shorter, equalling or little exceeding the apices of nutlets.

Species about 14, distributed from Iran to Central Asia, in mountains.

KEY TO THE SPECIES

a. Flowers white, nutlets appendiculate at the margins, appendages free at base, not forming a marginal wing. ..... 3. *L. albiflora.*
a. Flowers blue, nutlets appendiculate at the margins, appendages partly or completely confluent at base, forming a narrow or broad marginal wing.
  b. Nutlets broadly winged at margins, wings folded inside, inner margins of the wings scarious, entire to sometimes dentate. ..... 2. *L. microcarpa.*

b. Nutlets narrowly winged at margins, wings not folded inside, inner margins of the wings not scarious, usually dentate, teeth bearing glochidia at their apices. ..... 1. *L. inconspicua.*

1. **L. inconspicua** (Brand) Riedl, Oesterr. Bot. Zeitschr. **110**: 517. 1963; in Køie & Rechinger, Biol. Skr. **13**(4): 203. 1963; in Rechinger, Fl. Iranica **48**: 81. 1967.

Paracaryum inconspicuum Brand, Repert. Sp. Nov. **13**: 549. 1915; Pflanzenr. IV. **252** (Heft 78): 46. 1921.

TYPE: Afghanistan, *Griffith 5976* (K-holotype, GH-isotype).

ICON.: Riedl, l. c. **48**: *t. 18. fig. 1.* 1967.

Annual, decumbent to ascendent herb. Stems many from the base, up to 20 cm. long, simple to little branched, slender; stem and branches covered with soft, retrorsely appressed to subpatent trichomes ca. 0.2 mm. long, not arising from tuberculate bases. Basal leaves forming a rosette; basal and lower cauline leaves petiolate, petioles up to 20 mm. long, slender, hairy, with some thick, spreading trichomes at the margins to 2 mm. long, lamina oblong-ovate, to 30 mm. long and 15 mm. broad, gradually or sometimes abruptly narrowed towards the base, obtuse to roundish, loosely covered with white, soft, appressed trichomes to 0.2 mm. long on the upper surface, densely so on the lower surface, on the upper surface these intermixed with scattered long, stout, white trichomes arising from tuberculate bases; upper cauline leaves sessile, gradually reduced in size. Inflorescences short in flower, elongated in fruit, bracteate. Pedicels short in flower, elongated in fruit, bracteate. Pedicels in flower 1–2 mm. long, in fruit elongated to 10 mm., slender, hairy, recurved. Calyx divided nearly to the base, lobes 1.5 mm. long, hairy, erect, enlarged in fruit, oblong to broadly lanceolate, 2–3 mm. long, 1 mm. broad, pubescent on both sides and margins. Corolla blue, subtubular, 2 mm. long, lobes broadly ovate, patent; faucal appendages subquadrate. Stamens included; filaments very short, inserted at the middle of the corolla tube. Nutlets not more than 2 mm. long, ovoid, narrowly winged and denticulate at the margins, dorsal middle area tuberculate, tubercles short to long and glochidiate at apex. Style ca. 0.5 mm. long.

DISTRIBUTION: Iran, Afghanistan, West Pakistan.

West Pakistan: CHITRAL STATE: Brumboret Gol. N. of Drosh, 1500 m., *Bowes Lyon 647* (BM); *Stainton 2228* (BM); *Harriss 16387* (K); Chitral Mastuj tract, Kaghosi, 1500 m., *Stainton 2403* (BM).

The specimens cited above differ in some minor details from the type (*Griffith 5976*) collected in Afghanistan. In the type specimen the stems, petioles, and pedicels are all densely covered with short trichomes, which are not retrorsely appressed but spreading. Sepals in fruit are 3–4 mm. long, oblong, more or less obtuse at apex. In the specimens cited above the short trichomes on the stems, petioles, and pedicels are evidently re-

trorsely appressed and the sepals in fruit do not usually exceed 2.5 mm. (or rarely) 3 mm. They are broadly lanceolate and acutish at their apices.

Brand (l. c.) and Riedl (l. c.) have considered the species to be annual, but specimens collected by *Stainton* (*2403*, *2228*) appear to me to be perennials. On examining more material from the area the West Pakistan plants may prove to be a variation worthy of recognition.

2. **L. microcarpa** (Boiss.) Riedl, Oesterr. Bot. Zeitschr. **110**: 517. 1963; in Køie & Rechinger, Biol. Skr. **13**(4): 203. 1963; in Rechinger, Fl. Iranica **48**: 80. 1967.

Paracaryum microcarpum (Boiss.) Diagn. Pl. Orient. **3**: 139. 1856; Fl. Orient. **4**: 255. 1875; C. B. Clarke in Hook. f. Fl. Brit. India **4**: 162. 1883; Brand, Pflanzenr. IV. **252** (Heft 78): 46. 1921.

TYPE: Afghanistan: Hab. in regio Cabulico circa Choky et in sylvaticis Bharowul, *Griffith 5975* (K-holotype, GH-isotype).

Perennial, procumbent to ascendent herb. Stems many, 10–45 cm. long, simple or branched; stem and branches covered densely with white, patent trichomes to 2 mm. long, arising from prominent tuberculate bases. Basal leaves petiolate, petioles slender, pubescent to 50 mm. long; lamina oblong-lanceolate to oblong-ovate, entire, obtuse or sometimes acutish, to 50 mm. long and 20 mm. broad, covered on both surfaces with white, long, subappressed or, in the old leaves, more or less patent trichomes arising from white tuberculate bases; cauline leaves subsessile to sessile, gradually reduced in size upwards. Inflorescence short in flower, much elongated in fruit, lax, bracteate. Pedicels very short in flower, elongated to 13 mm. in fruit, slender, hairy, more or less reflexed. Calyx divided nearly to the base, lobes 1.5–2.5 mm. long and ca. 0.7 mm. broad in flower, oblong, erect, densely hairy, in fruit oblong-ovate, obtuse or sometimes acutish, enlarged to 4 mm. long and 1.7 mm. broad, pubescent externally, more or less glabrous inside, reflexed. Corolla blue, campanulate, 3–4 mm. long, tube equalling the limb, lobes broadly ovate, spreading, 1 mm. long, 1.7 mm. broad. Anthers included, inserted below the faucal appendages on the corolla tube. Nutlets brown, ovate, 2 mm. long, ca. 1.5 mm. broad, winged at the margins, wings inflexed and again folded outside, inner margins of the wings scarious, entire or sometimes dentate, middle dorsal area tuberculate, tubercles short (to sometimes long), bearing glochidia at apex, external surface smooth to slightly tuberculate. Style 1 mm. long, exceeding the nutlets by 0.5–0.7 mm.

DISTRIBUTION: Afghanistan, West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Ziarat, Lowari Pass, 2500 m., *Stainton 2558* (BM); Jambatai, *Harriss 16385* (K); Lowari Pass, *Siddiqui* in *R. R. Stewart 25448* (BM). KURRAM AGENCY: Kurram Valley, *Aitchison 106*, *117*, *197* (GH). SWAT STATE: mountains east of Kalam, 25 miles above Bahrain, 2200 m.,

Rodin 5683 (US); Bahrain to Kolaila, 1600–2200 m., *Lamond 1761* (E); *Rechinger 30693* (W). Reported from Baluchistan hills, *Stocks 738, 758*; Fort Sandeman, *Duthie 18931*; *Harsukh 20601*; Khyber Agency, Jamrud hills, *Siddiqui 2460*.

Kashmir: Kishenganga Valley, Kiran Nullah, 1800–2000 m., *R. R. Stewart 17538* (GH); Kiran to Reshna, 1800 m., *R. R. & I. D. Stewart 17689* (GH); Islampur, *Kazmi 293a* (PES); Chinari, *Kazmi s.n.* (PES). Miscellaneous: Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH). Reported from: Uri, *Meebold 4237*; Padar, *R. R. Stewart 2916*; Ferozpur Nullaha, *Nath 907*.

3. **L. albiflora** Riedl in Rechinger, Fl. Iranica **48**: 83. 1967.

TYPE: Afghanistan: Kataghan, near Salang, 3000 m., *Neubaur 4496* (W).

ICON.: Riedl, l. c. *t. 16. fig. 12*; *t. 18. fig. 5*. 1967.

Perennial, shrubby herb, to 15 cm. tall. Stems numerous, prostrate, to 25 cm. long, simple or slightly branched, covered loosely or densely with appressed or subpatent trichomes. Basal leaves oblanceolate to spathulate-lanceolate, entire, acute to obtusish, 30–50 mm. long, 3–6 mm. broad, gradually narrowed towards the petioles; petioles 1/3–1/2 the length of lamina; lower cauline leaves more or less like the basal leaves, upper cauline leaves abruptly reduced in size, sessile, lanceolate to linear-lanceolate, 12–20 mm. long, 2–4 mm. broad; all the leaves at first densely, later loosely covered with trichomes. Inflorescence usually terminal, rarely lateral, binate or ternate, congested, short in flower, elongated in fruit to 24 cm., bracteate, lower bracts to 9 mm., upper bracts to 2.5 mm. long, linear-lanceolate. Pedicels 1–1.5 mm. long in flower, elongated in fruit to 4.5 mm. Calyx divided to the base, lobes ca. 3 mm. long in flower, enlarged to 5(–5.5) mm. in fruit, 0.5 mm. broad, linear, acute, hairy, trichomes subappressed. Corolla white, infundibuliform-campanulate, 4–4.5 mm. long, tube 1 mm. long, limbs subpatent, 4 mm. in diameter, lobes suborbicular, 2 mm. long; faucal appendages 0.7 mm. long, narrow, rounded at apex. Nutlets 2–2.5 mm. long, ovate-pyramidal, brownish, appendiculate at margins, appendages few, free at base, 0.5–0.8 mm. long, erect, bearing glochidia at apex, dorsal middle area distinctly carinate, otherwise tuberculate. Style 1 mm. long.

DISTRIBUTION: Afghanistan, West Pakistan.

West Pakistan: Reported from: Kurram Valley: Mont. Sikaram, 3000 m., *Aitchison 107* (Riedl, l. c. **48**: 83. 1967).

I did not see any specimen of *Lepechiniella albiflora*, but from its original description it appears to be a well distinguished species. In our area it is related to *L. inconspicua* in the size and form of the nutlets, but differs in having much shorter (up to 4.5 mm.) pedicels in fruit, compared to the much longer (to 10 mm.) pedicels in *L. inconspicua*, much longer (5 mm.) and narrower (0.5 mm.) calyx lobes compared to

those of the latter species (2–3 mm. long and 1 mm. broad), and large, white corollas.

Both *Lepechiniella inconspicua* and *L. albiflora* may easily be distinguished from *Lepechiniella microcarpa* by their wings not folded at the margins of the nutlets.

17. Heterocaryum A. DC. in DC. Prodr. 10: 144. 1846.

Echinospermum Lehm. Sect. 1. *Heterocaryum* (A. DC.) Boiss. Fl. Orient. 4: 247. 1875.
Lappula § 2. *Heterocaryum* (A. DC.) Post & Kuntze, Lexicon 216. 1914.

TYPE SPECIES: *H. laevigatum* (Kar. & Kir.) A. DC. (lectotype species).

Annual decumbent or erect herbs. Stem, branches, and leaves covered loosely or densely with trichomes usually arising from tuberculate bases, rarely subglabrous. Inflorescence bracteate, elongating in age. Calyx divided to the base, lobes enlarged in fruit. Corolla infundibuliform to campanulate with 5 distinct trapeziform faucal appendages. Style very short, stigma capitate. Nutlets 4, homo- or heteromorphic, attached to a narrow columnar gynobase throughout their length, not separable, variously appendiculate or aculeate at margins.

Species 7, distributed from Turkey to central Asia.

KEY TO THE SPECIES

a. Fruits sessile to indistinctly short pedicellate. ..... 1. *H. subsessile.*
a. Fruits distinctly pedicellate, pedicels longer than the fruits, thick, fleshy.
  b. Plants with few scattered trichomes on the stem and leaf-margins; leaves ovate to oblong-ovate; pedicels usually recurved in fruit; nutlets with two series of appendages at the margins, dorsal middle area pubescent. ..... 2. *H. laevigatum.*
  b. Plants usually densely pubescent on stems, branches, and leaves; leaves linear to linear-lanceolate; pedicels usually erect in fruit; nutlets with a single series of appendages at the margins, dorsal middle area not pubescent.
    c. Plants robust, one pair of the long decurrent nutlets appendiculate at the margins and the middle dorsal area, appendages of the middle area sometimes longer than the marginal ones. ..... 3. *H. rigidum.*
    c. Plants weak, one pair of the long decurrent nutlets appendiculate at the margins, middle dorsal area plicate, plicae beaded, smooth, rarely appendiculate, appendages (if present) always shorter than the marginal ones. ..... 4. *H. szovitsianum.*

1. **H. subsessile** Vatke, Zeitschr. Ges. Naturw. 11: 129. 1875; Riedl in Rechinger, Fl. Iranica 48: 85. 1967.

Echinospermum oligacanthum Boiss. Fl. Orient. 4: 248. 1875, non Ledeb. 1846–1851.

Lappula echinophora var. *sessilis* O. Kuntze, Acta Horti Petrop. **10**: 215. 1887.
Cynoglossospermum oligacanthum (Boiss.) O. Kuntze, Rev. Gen. Pl. **2**: 436. 1891.
Echinospermum echinophorum (Pall.) Bernm. var. *sessile* Lipsky, Acta Horti Petrop. **26**: 539. 1910.
Heterocaryum echinophorum (Pall.) Brand var. *oligacanthum* (Boiss.) Brand, Pflanzenr. IV. **252** (Heft 97): 95. 1931.
Heterocaryum oligacanthum (Boiss.) Bornm. Beih. Bot. Centralbl. **59**–B: 306. 1939; M. Pop. in Fl. URSS. **19**: 546. 1953.

TYPE: In Persia orientali prope Shahrud et Ssertschah, *Bunge s.n.* (B).

Annual, erect herb to 35 mm. tall. Stems simple or divaricately branched; stem and branches pubescent, trichomes stiff, spreading. Basal and lower cauline leaves short petiolate, linear to linear-lanceolate, obtuse to acutish, 10–40 mm. long, 1–3 mm. broad, covered on both surfaces with stiff, appressed to patent, white trichomes arising from tuberculate bases, upper cauline leaves sessile, shorter, and narrower. Inflorescence leafy, short in flower, much elongated in fruit. Flowers sessile, fruits subsessile to very short (to 1.5 mm.) pedicellate. Calyx divided to the base, lobes in flower ca. 1 mm. long, linear, in fruit enlarging to ca. 5 mm. long, 1 mm. broad. Corolla blue, campanulate, ca. 2 mm. long. Fruits narrowly prismatic, 3–(4–5) mm. long, 2–3 mm. in diameter; nutlets heteromorphic, one pair of opposite nutlets longer, decurrent to the short pedicel, ca. 3.5 mm. long, 0.5–0.7 mm. broad, bearing 2–3 appendages at the lateral margins and 3–6 at apex, appendages 1–2 mm. long, glochidiate at apex, middle dorsal area longitudinally plicate, plicae swollen, beaded, glabrous or rarely with 1 or 2 prickles; the other pair of nutlets, excluding wings 2–2.5 mm. long, 0.5–1 mm. broad, not decurrent to the pedicels, bearing usually 2 appendages on the lateral margins and one at apex, appendages 1–2.5 mm. long, broadly triangular, confluent at base, forming marginal wings 0.2–1 mm. broad, puberulous, glochidiate at apex; wings dentate to aculeate at the margins, puberulous on both surfaces; dorsal middle area carinate, glabrous or sometimes slightly tuberculate to aculeolate. Style conspicuous, ca. 0.3 mm. long, stigma capitate.

DISTRIBUTION: Iran, Afghanistan, Turkestan, Pamir Alaj, West Pakistan.

West Pakistan: KALAT STATE: Chauki Guru, between Kalat and Mastung, *Jafri & Akbar 1820* (E). QUETTA DIST.: Chiltan mountains, between Dulai and Kanak, 1600 m., *Kazmi 1547* (PES); *Rechinger 29101* (W); Quetta to Chaman, 30 km. northeast of Quetta, low stony slopes, *Lamond 958b* (E).

2. **H. laevigatum** (Kar. & Kir.) DC. Prodr. **10**: 145. 1846; Ledeb. Fl. Rossica **3**: 164. 1847; Brand, Pflanzenr. IV. **252** (Heft 97): 97. 1931; M. Pop. in Fl. URSS. **19**: 539. 1953; Riedl in Rechinger, Fl. Iranica **48**: 88. 1967.

Echinospermum laevigatum Kar. & Kir. Bull. Soc. Nat. Moscou **15**: 411. 1842; Bunge in Reliq. Lehm. 411. 1851; Boiss. Fl. Orient. **4**: 248. 1875.

TYPE: In montosis apricis Songoriae ad rivulum Ai, nec non in fossis arenosis, prope fontem Sassyk-pastan, *Karelin & Kiriloff s.n.* (LE-holotype, GH-isotype).

ICON.: M. Pop. l. c. 19: *t. 26. fig. 2.* 1953.

Annual herb to 40 cm. tall. Stem simple or divaricately branched, glabrous or with few scattered, short, subappressed trichomes. Basal leaves few, ovate, subsessile, 15–20 mm. long, 8–12 mm. broad; lower cauline leaves, sessile, oblong-ovate, obtuse, 20–30 mm. long, 6–10 mm. broad, lower surface usually glabrous, upper surface, (especially at the margins) with few, scattered, short, soft, white trichomes arising from minute tuberculate bases; upper cauline leaves similar to the lower, shorter, narrower and acutish. Inflorescence short in flower, later much elongated, bracteate, bracts small. Pedicels 1–3 mm. long in flower, to 16 mm. long in fruit, horizontally patent or later recurved. Calyx divided to the base, ca. 1.5 mm. long in flower, enlarged in fruit, ca. 2.5 mm. long. Corolla blue, minute. Fruits ovoid, to 6 mm. long; nutlets 4, strongly heteromorphic, one pair of opposite nutlets much larger than the other, all nutlets similar in shape and bearing two series of appendages at their margins, the outer series composed of 3–4(–5) appendages at the lateral margins and one at the apex, sometimes with one or two very small ones between, appendages more or less dilated at base, 0.5–2 mm. long, reduced in length from the base of the nutlet to the apex, glochidiate at apex; inner series composed of numerous closely set appendages, not exceeding 0.5 mm. in length, more or less dilated at base, sometimes confluent and forming a narrow lacerated wing, dorsal middle area densely pubescent, carinate. Style very short; stigma capitate.

DISTRIBUTION: Iran, Afghanistan, USSR, West Pakistan.

West Pakistan: QUETTA DIST.: Sheila Bagh, on rocky slopes, *Kazmi 1538b* (PES); between Bostan and Saran Tangi, 1800 m., *Kazmi 1503b* (PES); *Rechinger 29196* (W).

The presence of two series of appendages at the margin and the densely pubescent middle dorsal area of the nutlets of *Heterocaryum laevigatum*, distinguish this species from all the others in our area.

3. **H. rigidum** DC. Prodr. **10**: 145. 1846; Ledeb. Fl. Rossica **3**: 163. 1847; M. Pop. Fl. URSS **19**: 540. 1953; Riedl in Rechinger, Fl. Iranica **48**: 87. 1967.

Echinospermum heterocaryum Bunge in Mem. Acad. Sci. St. Pétersb. **7**: 411. 1854.

E. szovitsianum Boiss. Fl. Orient. **4**: 248. 1875, *pro parte* non Fisch. & C. A. Mey. 1835.

E. minimum sensu C. B. Clarke in Fl. Brit. India **4**: 162. 1883, non Lehm.

Heterocaryum echinophorum (Pall.) Brand var. *minimum* (Lehm.) Brand Pflanzenr. IV. **252** (Heft 97): 95. 1931, *pro parte*.

TYPE: Sibiria altaica orientalis, *Karelin & Kiriloff 1951* (G-isotype).
ICON.: M. Pop. l. c. *t. 26. fig. 3.* 1953.

Annual, erect or decumbent herb, branched above the base, 15–36 cm. tall. Stem and branches brown, to 2 mm. in diameter, covered with antrorsely appressed, white trichomes to 0.5 mm. long, intermixed with stiff, patent trichomes, arising from tuberculate bases, 1–1.3 mm. long. Basal leaves sessile, linear, to 40 mm. long and 5 mm. broad, obtuse, covered loosely on both surfaces with white, stiff, patent trichomes 0.5–1.3 mm. long, arising from tuberculate bases; middle and upper cauline leaves similar to the basal ones, shorter and narrower. Inflorescence short in flower, much elongated in fruit, bearing fruits 5–15 mm. apart. Pedicels very short in flower, elongated in fruit to 10 mm., 1 mm. thick, gradually attenuated towards the base. Calyx divided to the base, lobes 1.5–2 mm. long, hairy, elongated in fruit to 3–5 mm. Corolla blue, campanulate, 2–2.5 mm. long, slightly exceeding the calyx. Fruits ovoid, 5–6 mm. long, 3–4 mm. broad; nutlets 4, heteromorphic, one pair of opposite nutlets oblong, ca. 5 mm. long, 1–1.5 mm. broad, decurrent to the pedicel, bearing 3–5 appendages at the lateral margins, 3–5 at their apices, dorsal middle area with two to three parallel rows of 3–7 appendages, appendages to 1.5 mm. long, not at all to slightly dilated at base, puberulous on the lower half, bearing glochidia at apex; nutlets of the other opposite pair, ovate, 3–4 mm. long, 1.5–2 mm. broad, not decurrent, bearing 3–4 appendages on the lateral margins, 1–3 at apex and 1 at base, appendages 0.5–1.5 mm. long, dilated at base, sometimes confluent, forming a narrow wing, glochidiate at apex, dorsal middle area carinate, tuberculate to minutely aculeate, not appendiculate; both types of nutlets usually tuberculate externally. Style very short, stigma capitate.

DISTRIBUTION: Iran, Afghanistan, USSR, West Pakistan.

West Pakistan: PESHAWAR DIST.: Peshawar, *Deane s.n.* (K). QUATTA DIST.: Khanai, 1800 m., *Duthie s.n.* (K); Sariab Road, 5 km. from Quetta, *Lamond 926* (E); Quetta, Pishni forest nursery and surroundings, *Kazmi 1435b* (PES). RAWALPINDI DIST.: Hurroo, *Aitchison 1085* (K).

Heterocaryum rigidum is closely related to *H. szovitsianum* from which it is distinguished by its decurrent pair of opposite nutlets which are appendiculate in the middle dorsal area, with appendages more or less the same as those on the margins.

4. **H. szovitsianum** (Fisch. & C. A. Mey.) DC. Prodr. **10**: 145. 1846; Ledeb. Fl. Rossica **3**: 163. 1847; M. Pop. Fl. URSS **19**: 546. 1953; Riedl in Rechinger, Fl. Iranica **48**: 86. 1967.

Echinospermum szovitsianum Fisch. & C. A. Mey. Index Sem. Hort. Petrop. **2**: 36. 1835; Boiss. Fl. Orient. **4**: 247. 1875, *pro parte.*
Heterocaryum pachypodum DC. Prodr. **10**: 144. 1846.
H. pachypodum DC. var. *kotschyanum* DC. Prodr. **10**: 145. 1846.

H. minimum (Lehm.) DC. var. *Szovitsianum* Regel, Acta Horti Petrop. **6**: 344. 1880.

Lappula echinophora var. *szovitsiana* O. Kuntze, Acta Horti Petrop. **10**: 214. 1887.

L. echinophora var. *pachypoda* O. Kuntze, *Ibid.*

L. szovitsiana (Fisch. & Mey.) Druce, List Brit. Pl. 50. 1908.

Heterocaryum echinophorum (Pall.) Brand var. *minimum* (Lehm.) Brand, Pflanzenr. IV. **252** (Heft 97): 95, 96. 1931, *pro parte*.

H. echinophorum (Pall.) Brand var. *pachypodum* (DC.) Brand, *loc. cit.* 96.

TYPE: In Persia boreali ad marginis agrorum, *Szovits s.n.* (LE).

ICON.: M. Pop. l. c. **19**: *t. 26. fig. 1.* 1953.

Annual, erect to subdecumbent branched herb, to 30 cm. tall. Stem and branches covered with stiff, usually patent to sometimes subappressed trichomes to 1.5 mm. long. Basal leaves linear, oblong-spathulate or sometimes ovate, obtuse, petiolate, petioles equalling the lamina, (including petioles) 10–30 mm. long, 3–6 mm. broad, covered loosely on both surfaces with stiff, usually patent, white trichomes to 1.5 mm. long, arising from tuberculate bases; cauline leaves sessile, lanceolate to linear-lanceolate, obtuse, to 40 mm. long and 7 mm. broad; upper cauline leaves shorter and narrower. Inflorescence leafy, elongating in age; pedicels 1–3 mm. long in flower, elongated in fruit to 11 mm., hairy. Calyx divided to the base, lobes 3–4 mm. long and 0.5 mm. broad in flower, linear, enlarging in fruit to 11 mm. long and 1.5 mm. broad. Corolla blue, campanulate 2.5–3.5 mm. long. Fruits ovoid, 4–8 mm. long, to 5 mm. broad; nutlets 4, heteromorphic, one pair of opposite nutlets, oblong, decurrent to the pedicel, 6–7 mm. long, 1–1.5 mm. broad, bearing 2–4 appendages at the lateral, thickened margins and 1–5 at the apices, appendages 0.5–1 mm. long, distant, not dilated at base, glochidiate at apex, dorsal middle area carinate, plicate, plicae swollen irregularly at places, glabrous; the other pair of opposite nutlets not decurrent, nutlets oblong, 5–6 mm. long, ca. 1.5 mm. broad, bearing 4–5 appendages at the lateral margins and usually 1 at apex, appendages 1–3 mm. long, much dilated and confluent at base, forming an irregular wing up to 1 mm. broad, glochidiate at apex, marginal wing and lower part of appendages pinkish brown, puberulous; dorsal middle area carinate, tuberculate, tubercles arranged longitudinally, glabrous or puberulous, rarely aculeolate. Style short, stigma capitate.

DISTRIBUTION: Turkey, Syria, Iraq, Iran, south and southwest USSR, Tien Shan, Afghanistan, West Pakistan, Kashmir.

West Pakistan: CHITRAL STATE: Birmogh Lasht, 2600 m., *Bowes Lyon 719* (BM); Drosh, 1200 m., *Stainton 2271* (BM). QUETTA DIST.: Pishni Forest Nursery and surrounding fields, *Kazmi 1425* (PES); environ de Quetta, *Schmid 1568* (MICH); Ziarat to Manna, 2600 m., *Jafri & Akbar 2192* (E). Reported from: NORTH WAZIRISTAN AGENCY: Datta Khel, *Blatter & Fernandes s.n.*

Kashmir: Miscellaneous: Himal. Bor. Occ., 6000 ped., Herb. Ind. Or. Hook. f. & Thoms., *Thomson s.n.* (GH). Reported from: Sumbal, *Meebold 4197.*

Riedl (in Rechinger, Fl. Iranica **48**: 89. 1967) has described *Heterocaryum* × *irregulare*, a hybrid between *H. rigidum* DC. and *H. macrocarpum* Zak. The new hybrid is based on a specimen (Kabul, Sher Darwasa, 1840m., *Gilli 3158*) collected in Afghanistan while the only other specimen cited is (Quetta, Sariab, 1700 m., *Rechinger 28840*) from West Pakistan. I did not see *Rechinger 28840* but have examined *Kazmi 1435b* and *Lamond 926*, which were collected at the same time and from the same locality with Professor Rechinger. These specimens are *H. rigidum* and show no affinity with *H. macrocarpum*. Moreover, as I did not find the other parent in this area, the presence of the hybrid in West Pakistan appears to be quite doubtful.

[*To be continued*]

THE GENERA OF CHRYSOBALANACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GHILLEAN T. PRANCE

CHRYSOBALANACEAE R. Brown in Tuckey, Narrat. Exped. Zaire Congo. 433. 1818, nom. cons.

Small trees [to large ones], shrubs or subshrubs, with simple, entire, alternate, stipulate, pinnately veined leaves. Inflorescence of terminal and subterminal cymose panicles or terminal and axillary cymules [racemose, spicate, paniculate]. Flowers perfect [rarely polygamous], perigynous, actinomorphic [to markedly zygomorphic]. Sepals 5, regular [often unequal], distinct, imbricate in aestivation. Petals 5 [rarely apetalous], inserted on margin of disc, equal in size [unequal], imbricate in aestivation [rarely clawed]. Disc always present, forming a lining to floral tube. Stamens numerous, 12–26 [few to numerous, 2–300], inserted around margin of disc [or unilaterally], all fertile [or some reduced to long or short staminodia]; filaments elongated filiform, free or united below up to half their length in small groups [short to elongated, rarely ligulately connate], slightly exserted beyond calyx lobes [included to far exserted], glabrous or pubescent; anthers bilocular at anthesis, longitudinally dehiscent; pollen medium sized, with 3 furrows [rarely 4], oblate-spheroidal to subprolate, triangular in polar view, with little wall patterning, scabrous to verrucose. Gynoecium unicarpellate [basically of three, but usually only one developed], inserted at base of floral tube [from base to mouth of floral tube], sessile [rarely with a short gynophore]; style single, basally attached; stigma 3-lobed [or truncate]; ovary superior, 1-locular with 2 basally attached erect anatropous ovules [rarely 2-locular with one ovule in each locule]. Fruit a fleshy [or dry] drupe. Seed lacking endosperm, embryo large, with plano-convex [or amygdaloid or ruminate] cotyledons. TYPE GENUS: *Chrysobalanus* L.

An almost exclusively pantropical family of 17 genera and about 430 species; only *Chrysobalanus* and *Licania* extend into the southeastern United States. The family is divided into tribes Chrysobalaneae and Hirtelleae; both genera of our area belong to the former.

The family has usually been considered to be a subfamily or tribe of

[1] Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB–6459X, principal investigator Carroll E. Wood, Jr.). The treatment in this paper, which is the 55th published in the series, follows the format established in the first paper (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References that have not been seen and verified are marked by an asterisk.

The plate was drawn by Miss Alma Hochhauser. I wish to thank Dr. Wood for his advice and helpful suggestions during the preparation of this manuscript.

the Rosaceae, but it is markedly distinct from that family, differing in the gynobasic style, the erect ovule, the tendency toward zygomorphic flowers, the rubiaceous stomata, the presence of silica, the pollen morphology, and in numerous anatomical features, especially the secondary xylem. The Chrysobalanaceae form a well-marked and natural family. Various phylogenists have suggested diverse relationships for the family but it seems to belong to the Rosales between the Rosaceae and Leguminosae. Small and a few other authors have placed the Chrysobalanaceae in the family Amygdalaceae, which consists of the Chrysobalanaceae and Rosaceae subfam. Prunoideae. This is, however, an unnatural grouping, and the Prunoideae clearly belong with the rest of the Rosaceae, rather than with the Chrysobalanaceae. The anatomy of these two groups is very different, and the morphological features given above also separate them.

The generic limits within the family have recently been redefined on a worldwide basis (Prance, 1969, & in press), and as now defined they are relatively distinct. The result of this work shows that two genera are represented in our area. One species previously considered a member of *Chrysobalanus* or as the separate genus *Geobalanus* has been transferred to *Licania*, a widespread, predominantly neotropical genus.

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KEY TO THE GENERA OF CHRYSOBALANACEAE IN THE SOUTHEASTERN UNITED STATES

Plants shrubs or small trees; staminal filaments pubescent, joined in small groups up to half their length; endocarp longitudinally ribbed (costate); inflorescences axillary. ..... 1. *Chrysobalanus*.

Plants suffruticose, low, colonial, spreading by woody underground stems; staminal filaments glabrous, connate at base only; endocarp smooth, not ribbed; inflorescences terminal and subterminal. ..... 2. *Licania*.

1. **Chrysobalanus** Linnaeus, Sp. Pl. 1: 514. 1753; Gen. Pl. ed. 5. 299. 1754.

Small to large shrubs, or rarely small trees, with coriaceous pinnately veined leaves, often with two glands at base of blade. Inflorescence few flowered, terminal or axillary, either a short raceme of cymules or cymose throughout, or, when consisting of about 6 flowers, a false raceme. Sepals acute, pubescent. Petals equaling sepals, glabrous, white. Stamens 12–26, exserted beyond sepals, some often shorter than others, inserted in a complete circle around disc [slightly unilateral]; filaments united in small groups for up to half their length [free almost to base], densely hairy. Style inserted at base of ovary, pubescent for most of its length; ovary pilose, inserted at base of floral tube, 1-locular, with two erect ovules.

FIGURE 1. CHRYSOBALANACEAE. a–j, **Chrysobalanus.** *C. Icaco*: a, habit, × ½; b, flower, × 4; c, flower in vertical section, × 4; d–h, petals, × 4; i, fruit, × 1; j, fruit in vertical section, × 1. k–t, **Licania.** *L. Michauxii*: k, habit, × ½; l, flower, × 4; m, flower in vertical section, × 4; n–r, petals, × 4; s, fruit, × 1; t, fruit in vertical section, × 1.

Fruit a small ellipsoid fleshy drupe, smooth, longitudinally ribbed; endocarp thin, hard, with 4–8 prominent longitudinal ridges corresponding to lines of fracture that allow the seedling to escape, glabrous within, filled by the large plano-convex cotyledons. Germination hypogeal. TYPE SPECIES: *Chrysobalanus Icaco* L. (Name derived from Greek *chrysos*, golden, and *balanos*, acorn or fruit.)

A primarily tropical genus of four species, two confined to Africa and one to the West Indies. The fourth, *Chrysobalanus Icaco*, cocoa plum, is a widespread coastal species from subtropical Florida through the Caribbean and Central America to eastern South America and West Africa. In the southern part of peninsular Florida *C. Icaco* is a common shrub or tree of beaches, sand dunes, coastal hammocks, hammock islands in the Everglades, and cypress-heads.

The extreme variation in leaf shape and size and fruit size in *Chrysobalanus Icaco* has led to the description of numerous taxa throughout its range (e.g., in our area, *C. interior* Small). There is, however, little correlation of the variable characters, and there seems to be no basis for recognition of more than one species. In at least Trinidad, Suriname, and Brazil, the different forms are frequently found growing side by side without any ecological separation (obs. Prance). The leaves vary from extremely small to large and from orbicular to elliptic, and both shape and size are quite variable on the same plant. The very variable fruit is from 0.8 to 4.5 cm. long. The larger fruits are more conspicuously ribbed than the smaller ones, and they tend to have a thicker, more fleshy mesocarp. In addition, the mature fruit may be deep red or purple to black or yellow. (To judge from the name of the genus, the material described by Linnaeus must have been of the yellow-skinned form.) The fruit is edible, but only the larger, more fleshy fruits borne by some plants make good eating, the differences in fruit type being comparable to those between good and bad varieties of plum (*Prunus domestica* L.). Where *C. Icaco* is used commercially there is obviously some selection of plants. For the present, it seems best to maintain only a single polymorphic species, for it is impossible to subdivide this species on the basis of herbarium material and ecology alone. An experimental study of plants of the different morphological types grown in controlled environments should yield much additional information. Attempts to examine the chromosomes of *C. Icaco* have thus far proved unsuccessful.

The fruits of *Chrysobalanus Icaco* are commonly used for preserves in Venezuela and Colombia, but only occasionally in our area. Plants of this species are sometimes grown as ornamentals.

Chrysobalanus is most closely related to *Licania*, a predominantly neotropical genus. The differences between the two are small, but a study of these genera on a worldwide basis shows that they are best kept apart. *Chrysobalanus* differs from *Licania* in the ridged endocarp of the fruit, in the hairy filaments that are joined together in small groups, and in the inflorescence.

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Under family references see BENTHAM & HOOKER (p. 606), BONNE (1928, pp. 163, 244–346, 356), FOCKE (p. 57), GRISEBACH (p. 229), HUTCHINSON, KÜSTER (pp. 135–137), PRANCE (1967, p. 216; 1970, in press), and SMALL (p. 645).

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2. **Licania** Aublet, Hist. Pl. Guiane Franç. 1: 119. *pl. 45*. 1775.

Subshrubs [shrubs to large trees] with coriaceous [membranaceous to chartaceous] pinnately veined leaves. Inflorescences rather lax branched terminal and subterminal cymose panicles [or a sparsely branched panicle of racemes, a panicle, or a spike]. Sepals acute [or rounded], pubescent [to glabrous]. Petals equaling sepals [larger or smaller than sepals, or absent], pubescent [glabrous]. Stamens 14–17 [3–40], exserted slightly beyond sepals [included to far exserted], inserted in a complete circle around disc [unilateral]; filaments united at base only [free to base], glabrous [rarely hairy, very short and included]. Style inserted at base of ovary, glabrous [to densely hairy]; ovary inserted at base of floral tube, usually 1-carpellate but sometimes 2 or 3 carpels developing, glabrous or sparsely hairy [to densely hairy], unilocular, with two erect ovules. Fruit a small ellipsoid drupe [to large and of varying shape], smooth, glabrous [sometimes verrucose, pulverulent or densely pubescent]; endocarp hard, thin [to thick] terete, not ridged, sparsely hairy [to densely hairy within], filled by the large cotyledons. Germination hypogeal. (Including *Moquilea* Aubl., 1775; *Hedycrea* Schreb., 1789; *Geobalanus* Small, 1913; and others.) TYPE SPECIES: *Licania incana* Aublet. (Name a misspelled anagram derived from the local name in French Guiana, *caligni*.)

Primarily a neotropical genus of 151 species, in three subgenera and eight sections, with one species widespread in Malesia and one confined to our area.

Licania Michauxii Prance,[2] gopher-apple or ground-oak, is a common

[2] Licania Michauxii Prance, nom. nov. *Chrysobalanus oblongifolius* Michx. Fl. Bor.-Am. 1: 283. 1811, non *Licania oblongifolia* Standl., 1917; *C. retusus* Raf. New Fl. N. Am. 3: 26. 1838, non L. retusa Pilger, 1914; *C. incanus* Raf. loc. cit., non *L. incana*

suffruticose shrub with spreading underground stems. It is abundant in pinelands and oak scrubland and on sand hills and sand-dunes in Florida and extends westward to Louisiana and northward to South Carolina. The full reasons for treating this species as a *Licania* instead of a *Chrysobalanus* will be given elsewhere (Prance, in press). The two genera are very closely related but are distinct when *L. Michauxii* is transferred from *Chrysobalanus* to *Licania*. It falls well within the limits of *Licania*, and there are no grounds whatever for regarding it as a separate genus. It is a member of subg. MOQUILEA (Aubl.) Prance (Atas Simp. Biota Amazôn. **4**: 224. 1967), sect. MOQUILEA (Aubl.) Prance,[3] and it is most closely related to *L. retifolia* Blake, of Mexico.

This species has previously been included in both *Chrysobalanus* L. and *Geobalanus* Small. Its synonyms include *C. oblongifolius* Michx., *C. retusus* Raf., *C. incanus* Raf., *G. oblongifolius* (Michx.) Small, *G. pallidus* Small, and *C. pallidus* (Small) L. B. Sm. Since the specific epithets of all these combinations are already occupied in *Licania* (i.e., *L. incana* Aubl., *L. pallida* Spruce ex Sagot, *L. oblongifolia* Standl., and *L. retusa* Pilger) a new epithet was required. *Chrysobalanus prunifolius* Raf. has commonly been referred to this species, but type material has not been found, and the small leaves, few-flowered racemes, and podlike fruit described for *C. prunifolius* are quite unlike those of *L. Michauxii*.

The differences given by Small for his *Geobalanus pallidus* (leaves densely white-tomentose beneath, ovary pubescent, drupes 3–4 cm. long *vs.* leaves and ovary glabrous, fruit 2–2.5 cm. long in *G. oblongifolius*) do not hold. There is a gradation in the pubescence of both the ovary and the leaf undersurface, and in many cases the pubescence of the leaf is caducous and the older leaves are glabrous. *Chrysobalanus incanus* Raf., based on the variant noted by Michaux under his *C. oblongifolius*, represents the same pubescent form, which, although conspicuous in its extreme development, does not seem to be worthy of taxonomic rank.

Licania Michauxii has often been said to have a stellate pubescence, but it does not. This erroneous report, attributable to Küster, has led to the mention of stellate pubescence in connection with the family in several other publications. The mistake is based on a mixed collection of

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Aubl., 1775; *Geobalanus pallidus* Small, Fl. Miami 81. 1913, non *L. pallida* Spruce ex Sagot, 1883, nec *L. pallida* Britton, 1890.

[3] **Licania** Aubl. sect. **Moquilea** (Aubl.) Prance, comb. nov. *Moquilea* Aubl. Hist. Pl. Guiane Franç. **1**: 521. *pl. 208*. 1775.

This sectional combination, cited without an author, was used under *Licania* subg. *Moquilea* (Aubl.) Prance in 1967 (Atas Simp. Biota Amazôn. **4**: 225), since this was the correct procedure under Art. 22, International Code of Botanical Nomenclature, 1966. However, changes adopted at the 11th International Botanical Congress, Seattle, 1969, restrict this tautonymic principle to the subgenus and section that include the type of the genus, but recommend that when a new epithet is needed in other subgenera and sections the repetitive principle be retained when possible. In conformity with these changes the combination *Licania* sect. *Moquilea* is made here formally and is cited with authors.

herbarium material. The widely distributed *A. H. Curtiss 727* includes, in addition to *L. Michauxii*, sterile branches of *Quercus pumila* Walt., a plant that has stellate hairs on the lower leaf surface. *Quercus pumila* may have the same suffruticose habit as *L. Michauxii*, and sterile specimens could easily be mistaken for it, except for their stellate pubescence.

Licania is most closely related to *Chrysobalanus* (*q. v.*). It is also close to the African *Afrolicania* Mildbr. and the Malesian *Parastemon* A. DC. Together the four comprise the tribe Chrysobalaneae, which is distinguished by the regular flowers with a basally inserted gynoecium.

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Under family references see BONNE (1928, pp. 164, 347, 348), FRITSCH, HUTCHINSON (p. 191), KÜSTER (pp. 137, 194–201), PRANCE (1967, pp. 224–227; 1970, in press), and SMALL (p. 645, 646, as *Geobalanus*).

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A NEW SPECIES OF PARIETARIA (URTICACEAE) FROM NORTHEASTERN MEXICO [1]

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DURING A GENERAL REVIEW of the collection of *Parietaria* in the combined herbaria of the Arnold Arboretum and Gray Herbarium, an undescribed species, variously named *P. debilis* Forst. f., *P. floridana* Nutt., *P. obtusa* Rydb., *P. officinalis* L., and *P. pensylvanica* Muhl. ex Willd., was recognized among Mexican material. Examination of additional specimens borrowed from other herbaria has established its presence in three, probably four, states in northeastern México.

A genus of about 20 species in two subgenera, *Parietaria* is largely restricted to temperate and subtropical latitudes (or if nearer the equator, then usually montane), with the bulk of the genus occurring in Europe and North America. Regrettably, no monograph has appeared since publication of Weddell's treatment (1869) in the De Candolle *Prodromus*.

A major taxonomic problem in this genus, pertaining especially to the widespread species, has been the interpretation of the extensive variability in leaf and bract size, pubescence, and habit. Hedberg (1957), for example, stressing the intergradations of vegetative characters in the four Parietarias reported from the mountains of east Africa, concluded that three of them could be accommodated within the fourth, the wide-ranging *Parietaria debilis*. In my own experience, and as has been recently emphasized by the work of Hinton (1968, 1969) and Townsend (1968), vegetative characters may or may not be satisfactory from the taxonomic standpoint, but achene shape and form of the accrescent perianths developing from both perfect and carpellate flowers (should the latter be present) provide the most stable and, therefore, the most useful diagnostic features.

Parietaria decoris N. G. Miller, sp. nov.

Herbae perennes (?). Caules ascendentes numerosi vel singulares trichomatibus et longis laxisque et brevioribus uncatisque sparse vel dense vestiti. Folia petiolata alterna vel opposita vel in plantis juvenilibus sub-

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opposita; laminae ovatae ad basin cuneatae infra pilosae; nervi laterales prominentes suboppositique pinnatim in paribus duobus dispositi, uno e basi costae, altero e medio exoriente; cystolithi bacilliformes non nisi in pagina supera folii praesentes. Inflorescentiae cymulosae pauciflorae et bracteatae; bracteae discretae linearesque ad apicem obtusae, ciliis et cystolithis bacilliformibus instructae, quam perianthium fructum maturum cingens breviores. Flores perfecti; perianthium viride uniseriale ad basin tubulare autem apicem versus lobos 4 libros praebens; stylus 1 apicalis filiformisque stigmate lineare. Achenia fusca subovoidea symmetrica bilateraliter, ventricosa, per basin persistentem stylo apiculata. Perianthium accrescens; pars infera (½–⅔ longitudinis totae) fusca, 4-angulata et in quoque angulo trichomatibus numerosis lenibusque extrinsecus patentibus praedita; pars supera ex lobis naviculiformibus viridibus, his trichomatibus uncatis cystolithisque bacilliformibus instructis, constata.

Holotypus: *C. H. & M. T. Mueller 645* (GH).

Many- or single-stemmed, ascending, perennial (?) herbs. Stems green, sometimes reddish, sparsely to densely covered with long, lax hairs and shorter hooked ones. Leaves petiolate, alternate or opposite to subopposite in young plants; blades ovate, with a cuneate base, size variable, (1.4–) 2.2–5.8(–6.5) cm. long, (0.7–)1.0–3.0(–3.9) cm. wide, weakly pilose; venation pinnate, 2 pairs of prominent, subopposite lateral veins per leaf, one pair originating from near the base of the blade, the other near the middle; *cystoliths bacilliform* (rarely ovoid or spherical), restricted to the adaxial leaf surface. Inflorescences few-flowered bracteate cymules, two per node, one borne on either side of the petiole base; bracts separate, linear, ciliate, apex blunt, bacilliform cystoliths prominent, bracts shorter than the perianth surrounding the mature fruit. Flowers perfect, strongly protogynous; perianth green, uniseriate, fused basally, but with 4 free, apical lobes, which remain cupped around the stamens until pollen dispersal; stamens 4, filaments inflexed, anther sacs caducous, filaments remaining within the enlarging perianth; gynoecium unicarpellate, stipitate; style 1, apical, filiform, constricted near the ovary apex, stigma linear; style (and stigma) falling off before pollen is shed. Achene shiny, brown, ± ovoid, 1.0–1.3 mm. long, 0.6–0.8 mm. wide, *bilaterally symmetrical, ventricose, stipe off-center in lateral view* (see FIGURE 1, h); style base persisting as a short, hard, ± apical projection. Accrescent fruiting perianth loosely surrounding the mature achene, both probably dispersed together; *continuous basal portion brown, 4-angled, with abundant, soft hairs projecting outward from the angles, apical lobes green, boat-shaped, bearing hooked hairs and bacilliform cystoliths.* (Name from Latin, ornamented, in reference to the lobes of the accrescent perianth.)

Specimens examined. **México.** COAHUILA: La Mariposa Ranch, Muzquiz, *Marsh 1040* (TEX; see following comment). NUEVO LEÓN: In dense, moist wood, waterway below Alamar, ca. 15 mi. sw. of Galeana, 4500–5000 ft., *Mueller & Mueller 645* (holotype GH, isotype MICH); growing on side of cliff, oak zone,

Quelite, Cerro de la Silla near Monterrey, ca. 3800 ft., *White 1489* (GH, MICH); Hacienda Vista Hermosa, 35 mi. s. of Monterrey, ca. 2400 ft., *idem 1567* (mounted with one plant of *Parietaria pensylvanica*, GH); cliff in limestone canyon, El Diente Canyon, s. of Monterrey, 1200–1300 m., *Pennell 16869* (NY, US); wooded ravine, Horse Tail Falls, Santiago Municipality, *Chase 7782* (GH, MICH); moist cracks in rock, "chute" below cave, Huasteca Canyon, ca. 15 mi. se. of Monterrey, *Ward 5727* (MICH); Sierra Madre Mountains, Monterrey, *Mueller & Mueller 58* (GH); Guajuco, *Palmer 1266* (GH, NY) [as *P. officinalis* L. ?, see S. Watson, Proc. Am. Acad. **18**: 155. 1883]; outside entrance to grotto in Canyon Huajuco, e. of Villa Santiago, *Johnson & Barkley 15158M* (GH, NY, UC); limestone soil of Cañon Huajuco, e. of Villa Santiago in the Río San Juan valley, *idem 15148M* (GH), *16152M* (NY). TAMAULIPAS: On gravelly sand in open sun, mountains along Rt. 70, ca. 8 mi. s. of Ciudad Victoria, *King 4520* (MICH, NY, UC, US); on rich sand near streams or in cañons, near Victoria, 400 m., *Runyon 951* (TEX, US); Cerro de los Armadillos, vic. San José, Sierra de San Carlos, *Bartlett 10228* (MICH, US). SAN LUIS POTOSÍ: Tropical forest, El Salto, *Kenoyer & Crum 4031* (A, MICH); Tamasopo Cañon, *Pringle 5085* (GH, MEXU); rocky limestone woods, Espinazo del Diablo, Tamasopo Canyon, 800–900 m., *Pennell 17958* (US).

The (1) bilaterally symmetrical, ± apiculate, ventricose achenes, (2) bacilliform cystoliths borne in cells of the upper leaf epidermis (and best observed in dried plants), and (3) accrescent perianths in which four green, boat-shaped apical lobes contrast with the brown, tubular, basal portion of the calyx serve to distinguish *Parietaria decoris*. In shape and coloration, the accrescent perianths of this species are similar to those of *P. macrophylla* Robins. & Greenm., a species of southern México, which, however, in addition to other differences has black rather than brown achenes.

During the period of stigma receptivity, the stamens remain minute and the perianth increases only slightly in size. Until explosive pollen dispersal, which occurs sometime after the style has fallen off, the maturing inflexed stamens are confined by the enlarged perianth lobes. The overall lengthening of the perianth following anther dehiscence apparently occurs in the tissues comprising the basal, tubular portion of the perianth.

As far as I know, the bacilliform shape of the cystoliths is unique among described North American species, which otherwise have only punctiform markings. Indeed, cystoliths other than the punctiform type are unusual in the 4 or 5 genera and about 25 species that comprise the rest of tribe Parietarieae Gaud.

Leaf-cystoliths in plants from shaded, forest sites may be up to 8 times longer than wide, but in plants from open habitats where exposure to the sun is maximal (e.g., *King 4520*), there is a pronounced decrease in the cystolith length/width ratio. Associated with this change is a decrease in leaf size (cf. a, b, & c in FIGURE 1). However, in sun-grown plants most leaf-cystoliths remain clearly longer than wide, and the characteristic organization of the lateral veins is retained in the leaves of such plants. Based on the apparent rarity of bacilliform cystoliths within the genus, the Marsh collection from Coahuila (see above), consisting of only 2

FIGURE 1. **Parietaria decoris.** a, leaf, shade-grown plant (*Kenoyer & Crum 4031*, A), × 1; b, same (*Mueller & Mueller 645*, GH, holotype), × 1; c, leaf, plant grown in full sun (*King 4520*, MICH), × 1; d, cystoliths on adaxial leaf surface, shade-grown plant (holotype), × 25; e, flower, stigma presumably receptive at this stage but stamens minute and obviously immature (*King 4520* MICH), × 25; f, accrescent perianth, note cystoliths in apical lobes (holotype), × 12; g, detail of perianth base just prior to abscission of achene, perianth mostly removed, three filaments not shown (holotype), × 25; h, lateral view of achene (holotype), × 25; i, achene, rotated 90° counterclockwise from view shown in h (holotype), × 25.

juvenile plants without achenes and accrescent perianths, has been provisionally named *P. decoris*. Unfortunately, it is the only specimen from Coahuila assignable to this species to have come to my attention.

Parietaria decoris can be placed, somewhat unsatisfactorily, in subg. PARIETARIA (subg. *Euparietaria* Komarov in Jarmolenko), members of which have elongated styles and either all flowers of the cymule perfect or the lower ones carpellate and the rest perfect (Jarmolenko, 1936; see also Paclt, 1952). Most species belonging here are perennials. Although Jarmolenko's map (1941) shows this subgenus to be restricted to Europe and the Middle East, the New World *P. macrophylla* has an elongated

style (with a linear stigma), which is, incidentally, identical to the type occurring in *P. decoris*. However, the stigmatic apparatus of these two Mexican species differs from the exceptionally thin, glabrous style and the brush-like, apical stigma characteristic of the Old World members of the subgenus. The significance of the two types must await a reevaluation of the infrageneric classification of the genus.

Only a very short style, or none at all, supporting a somewhat flattened penicillate stigma, occurs in members of subg. FREIREA (Gaud.) Komarov in Jarmolenko (later treated as a genus by Jarmolenko, 1941). Lower flowers of an inflorescence are perfect, while upper ones are carpellate. Only annuals, including *Parietaria pensylvanica*, which ranges across the United States and southern Canada, southward into México, belong to this subgenus. Achenes of *P. pensylvanica*, although brownish, are non-ventricose.

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CHROMOSOME NUMBERS IN THE JUGLANDACEAE

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THE JUGLANDACEAE ARE CHARACTERIZED by trees having alternate and pinnate leaves with short-stalked or sessile leaflets. Plants monoecious, flowers unisexual, the staminate flowers in catkins on the twigs of the previous year; perianth typically 4-lobed, sometimes irregularly lobed, 3–many stamens; carpellate flowers solitary or in a small cluster or spike with inferior, bicarpellary, syncarpous, unilocular, or incompletely 2–4-celled ovary having one erect orthotropous ovule, style short with 2 stigmas. Fruit a drupe or a nut.

A small family of seven genera and about 60 species (Willis, 1966), distributed mostly in the North Temperate zone and in tropics of both hemispheres. *Carya* Nutt., the largest genus of the family, has 25 species distributed in eastern North America, Mexico, and eastern Asia. Fifteen species of *Juglans* L. are met in North America, the Andes, and from southeastern Europe to eastern Asia. The majority of the species of *Pterocarya* Kunth are confined to China and Japan. *Engelhardia* Lesch. ex Bl.[1] with five species, ranges from the Himalayas to Southeast Asia. *Oreomunnea* Oerst.,[2] *Platycarya* Sieb. & Zucc., and *Alfaroa* Standl. are small genera distributed in Mexico, China, and Costa Rica respectively.

For its size the family is of much economic value. *Juglans regia* L. (English or Persian Walnut), *J. nigra* L. (Black Walnut), and *J. cinerea* L. (Butternut) produce invaluable and decorative woods which are in much demand for cabinet and furniture making. The species of *Carya* Nutt. yield tough and elastic wood. To a limited extent, *Engelhardia* Lesch. ex Bl. is the source of timber in eastern Asia. The nuts of *Juglans* L. and *Carya* Nutt. are rich in oil and very nutritious.

The significant contribution in the field of cytology of the Juglandaceae had been that of Woodworth (1930), who analyzed the meiotic behavior of several species belonging to three genera. This paper presents chromosome numbers in the two genera, *Juglans* L. and the primitive, tropical genus *Engelhardia* Lesch. ex Bl., in an effort to get a clue to the base number and phylogeny of the family; and as a prerequisite for tree improvement through a rational breeding program.

MATERIAL AND METHODS

The material for meiotic studies was collected during 1965, from wild populations near Darjeeling (eastern Himalayas), Digboi (Assam), and

[1] Spellings adapted from Dilmy (1955).

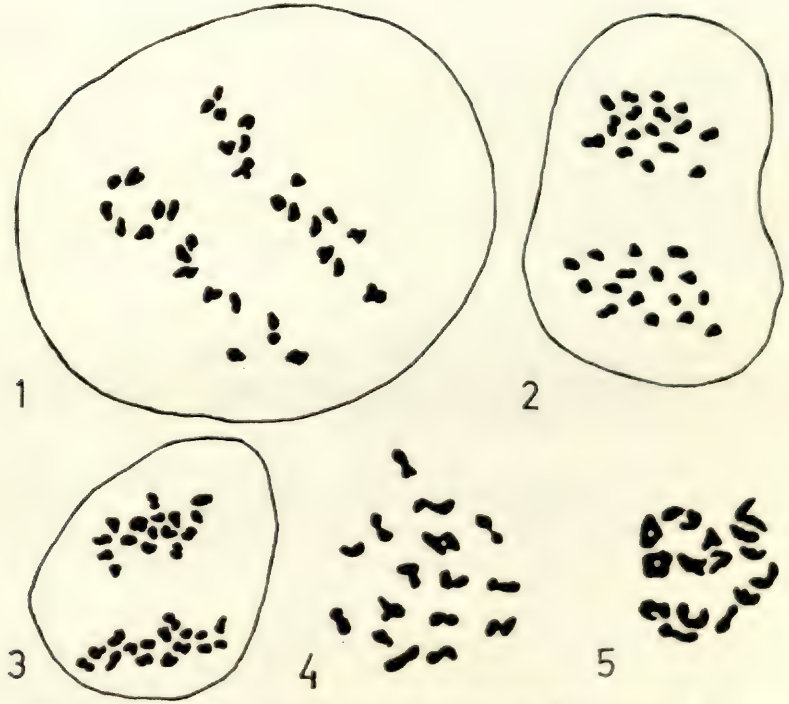
[2] Segregated from *Engelhardia* Lesch. ex Bl. by Leroy (1955) and Hjelmqvist (1960).

Shillong (Khasia and Jaintia hills). The exact source of material is given in TABLE 1. The flower buds were fixed in Carnoys fluid and then transferred to 95 percent alcohol. The anthers were squashed in 1 percent acetocarmine and the slides made permanent in Euparal. Camera lucida drawings were made at a magnification of 1350 ×. The voucher specimens are deposited in the Herbarium, Panjab University, Botany Department, Chandigarh, India.

OBSERVATIONS

The results of cytological studies on three species and two varieties are presented in TABLE 1.

Juglans regia L.: A lofty, deciduous tree up to 30 m. in height and, on the average, 3.5 m. in girth. Bark grey, longitudinally fissured. Found in the Himalayas from 900–3000 m., extending eastward to Burma and westward to Baluchistan. Extensively cultivated for its prized wood and edible nut.



FIGURES 1–5. Meiotic chromosomes in *Juglans* and *Engelhardia*, all, × 1350. 1. *J. regia*: M-II, $n = 16$; 2. *E. spicata* var. *colebrookeana*: A-I, $n = 16$; 3. *E. spicata*: M-II, $n = 16$; 4. *E. spicata* var. *aceriflora*: M-I, $n = 16$; 5. *E. roxburghiana*: M-I, $n = 16$.

FLOWER: February to April. FRUIT: September to October.

At M-II, 16 chromosomes were observed at each pole (FIGURE 1) and pollen formation was normal.

Engelhardia Lesch. ex Bl.: All the available Indian species and varieties of *Engelhardia* Lesch. ex Bl. were worked out. *Engelhardia* "*acerifolia* Bl." "*E. colebrookiana* Lindl.", as treated by Hooker (1885), are recognized by Manning (1966) as varieties of *E. spicata* Lesch. ex Bl., and his treatment has been followed.

Engelhardia spicata Lesch. ex Bl.: A large, deciduous tree up to 30 m. in height. Bark grayish-brown, rough, exfoliating in small flakes. Trees of this species are invariably loaded with climbers, epiphytic ferns, and orchids. Distributed in the sub-Himalayan region from Nepal eastward, and ascending up to 1800 m.

FLOWER: September to October. FRUIT: March to April.

Cytological analysis revealed 16 chromosomes at M-II at the two poles (FIGURE 3). Meiosis was perfectly normal.

Engelhardia spicata Lesch. ex Bl. var. **aceriflora** (Reinw.) Kds. & Val. (= *E. aceriflora* (Reinw.) Bl.): A large, deciduous tree in Sikkim, the Himalayas, and Khasia and Jaintia hills.

FLOWER: March to April. FRUIT: June to August.

Sixteen bivalents were observed at M-I (FIGURE 4). Meiosis was normal.

Engelhardia spicata Lesch. ex Bl. var. **colebrookeana** (Lindl. ex Wall.) Kds. & Val. (= *E. colebrookeana* Lindl. ex Wall.): A small, deciduous tree with spreading crown; bark brown, fibrous and light red with white streaks inside. Distributed from Chenab to Nepal, also in Assam, Khasia and Jaintia hills, and Burma.

FLOWER: February to March. FRUIT: April to June.

Sixteen chromosomes were observed at each pole at A-I (FIGURE 2). Meiosis and pollen formation was normal.

Engelhardia roxburghiana Wall. (= *E. wallichiana* Lindl.): A large tree up to 25 m. in height, met in Assam and Khasia and Jaintia hills, growing abundantly in the second storey of tropical wet evergreen forests of Upper Assam, and ascending up to 1000 m. in Khasia and Jaintia hills, where trees grow scattered.

FLOWER: April to May. FRUIT: June to July.

At M-I, 16 bivalents were revealed (FIGURE 5) and meiosis was normal.

DISCUSSION

All the presently investigated taxa of Juglandaceae uniformly show $n = 16$. Sixteen is suggested as the base number of the primitive genus

TABLE 1. List of the investigated taxa with their localities, chromosome numbers, and results of previous authors

NAME	LOCALITY	CHROMOSOME NUMBER	PREVIOUS REPORT
1. *Juglans regia*	Darjeeling: Lopchu 1500 m.	$n = 16$	$n = 16$ (Woodworth, 1930) from Arnold Arboretum; (Delay, 1947); (Mehra & Singh, 1962) from W. Himalayas
2. *Engelhardia spicata*	Darjeeling: Mahanadi 1300 m.	$n = 16$	$n = 16$ (Mehra & Gill, 1968) from W. Himalayas
	Lopchu 1500 m.	$n = 16$	
3. *E. spicata* var. *aceriflora*	Darjeeling: Rongtong 300 m.	$n = 16$	
4. *E. spicata* var. *colebrookeana*	Shillong: Garampani 750 m.	$n = 16$	
5. *E. roxburghiana*	Digboi: Upper Dehing Reserve Forest 150 m.	$n = 16$	
	Shillong: Nongpoh 350 m.	$n = 16$	

Engelhardia. The other genera, *Carya*, *Juglans*, and *Pterocarya* are also based on $x = 16$ (Darlington & Wylie, 1955). All the known taxa are diploid except a few tetraploid species of *Carya* (Woodworth, 1930), thus raising the polyploid figures to about 18 percent. Like the Lauraceae, the Fagaceae, and the conifers, the speciation in the majority of the Juglandaceae seems to have taken place at the diploid level.

Stebbins (1938, 1947, 1950) thinks that $x = 10$ and the higher base numbers are either primary or secondary numbers of polyploid origin; and he postulated their derivation by polyploidy from woody tropical genera yet unknown cytologically or from the extinct types. The Juglandaceae with $x = 16$ could be visualized to have been derived through polyploidy during the Cretaceous or early Tertiary period either from the Myricaceae having $x = 8$ — an interrelationship also suggested by Hjelmqvist (1948) on morphological grounds, or from the Corylaceae ($x = 8$) as cytologically evidenced by Woodworth (1930). If the above view holds, Hutchinson's (1926) system of classification which completely separates the Juglandaceae from the Amentiferae will need some rectification.

SUMMARY

The cytological investigations of all the available Indian taxa of the Juglandaceae reveal that $n = 16$ and the plants are diploid. The base number 16 is suggested for the genus *Engelhardia*. Stebbins's (1938, 1947, 1950) view of derivation of higher base numbers by polyploidy from unknown woody genera is upheld. Unlike Hutchinson's (1926) treatment of Juglandaceae, chromosomal data at hand favor the inclusion of the Juglandaceae in the Amentiferae near the Myricaceae and the Corylaceae.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 13. PHYTOCHEMICAL SCREENING AND LITERATURE SURVEY

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AS PART OF A DETAILED STUDY on the restricted flora of the elfin forest on the summit of Pico del Oeste, thirty-five species of plants were screened for the presence of three phytochemical constituents, alkaloids, saponins, and tannins. The literature was reviewed to determine which of these constituents had previously been found in the species cited or in related ones.

MATERIAL AND METHODS

PREPARATION OF EXTRACTS: The screening procedures for alkaloids, saponins, and tannins were adapted from those described by Wall *et al.* (1, 2). An extract of each plant sample was prepared by refluxing 50 grams of the air-dried, milled plant material with 300 ml. of 80 percent ethanol for one hour. Each extract was then cooled to room temperature, filtered by suction, and the residue was washed with sufficient 80 percent ethanol to bring the volume of filtrate to 500 ml.

Alkaloids. Fifty ml. of each extract was evaporated to dryness using a steam bath after which the residue was stirred with five ml. of 1 percent aqueous hydrochloric acid. One ml. of the filtrate was treated with a few drops of Mayer's reagent and a separate one ml. portion was treated similarly with silicotungstic acid reagent (12 percent aqueous). Precipitation or turbidity with either of these reagents was taken as preliminary evidence for the presence of alkaloids in the extract being evaluated. A confirmatory test, designed to remove non-alkaloidal compounds capable of eliciting "false-positive" reactions with either of these reagents was conducted in the following manner with all extracts giving a preliminary positive test for alkaloids.

Two ml. of the acidic aqueous extract, prepared as described above, was treated with 28 percent ammonium hydroxide solution until the solution was distinctly alkaline to litmus paper, and then extracted several times with chloroform. The chloroform extracts were combined and concentrated *in vacuo* to *ca.* two ml., then extracted with an equal volume of 1 percent aqueous hydrochloric acid. One ml. of the separated acid extract was treated with a few drops of Mayer's reagent, and a second one ml. portion was treated with silicotungstic acid reagent as previously described. Turbidity or precipitation after the addition of either of these reagents was taken as a confirmed positive test for the presence of alkaloids in the extract. The results of these tests are presented in TABLE 1.

Each plant sample was also screened for alkaloids using thin-layer chromatography according to the method of Farnsworth and Euler (3). This procedure was modified only in that the final volume of fraction I (chloroform extract) applied to each thin-layer plate was 30 μl. The results from this test are also presented in TABLE 1.

Saponins. Since all saponins, whether steroidal or triterpenoid, will hemolyze red blood cells, utilization of this property is advantageous for detecting this class of compounds in plant material. A red blood cell suspension was prepared and standardized against digitonin according to the protocol of Wall *et al.* (2). One ml. of each plant extract was mixed with 10 ml. of the red blood suspension and the mixtures were allowed to stand for one hour before observing the results. Complete hemolysis of the red blood cells in any instance was taken as evidence for a positive test, the results of which are presented in TABLE 1.

Tannins. 100 ml. of the original 80 percent ethanol extract from each plant sample was evaporated to dryness on a steam bath and the residue was stirred with 25 ml. of distilled water and filtered. Two ml. of the filtrate was treated with a few drops of gelatin-salt reagent (1). Precipitation along with a color reaction following the addition of ferric chloride reagent (blue-black, black, green-black) was positive evidence for the presence of tannins, green-black indicating tannins of the catechol type and black indicating tannins of the pyrogallol type. No precipitation with the gelatin-salt reagent and a green color with ferric chloride indicated the presence of phenolic compounds but not necessarily tannins. Precipitation with the gelatin-salt reagent and a brown color with ferric chloride indicated no tannins present.

SUMMARY

Of the thirty-five species of plants tested, alkaloids alone were found in two, alkaloids and tannins in three, saponins alone in one, saponins plus tannins in one, and tannis alone in thirteen. The remaining fifteen species contained none of these compounds although at least three gave tests for phenolic compounds.

With the exceptions of a report of alkaloids on *Lobelia portoricensis* and earlier work on *Cecropia peltata*, no published phytochemical data for any of the species of the test site were found. Our findings of alkaloids in *Hillia parasitica* and *Psychotria berteriana* are consistent with earlier reports of the presence of these constituents in other species of the same genera. On the other hand, our sample of *Ilex sintenisii* gave no evidence for the presence of caffeine and tannin for which *I. paraguariensis* is well-known. Alkaloids found in other species of *Justicia*, and the alkaloids, saponin, and tannin reported for other species of *Carex*, were not found in *Justicia martinsoniana* or *Carex polystachya* respectively.

TABLE 1. **Results of Phytochemical Screening**

[Literature references are to reports of various constituents for these or related species]

SCIENTIFIC NAME	PART[a] USED	ALKALOIDS[b] M[c]	ALKALOIDS[b] S[d]	ALKALOIDS[e] Fraction I	ALKALOIDS[e] Fraction II	TANNINS Gelatin salt	TANNINS $FeCl_3$[f]	SAPONINS	LIT. REF.
ACANTHACEAE									
Justicia martinsoniana	wp	–	–	–	–	–	–	–	(6–12)
AQUIFOLIACEAE									
Ilex sintenisii	st/lf	–	–	–	–	+	br	–	(13–34)
BIGNONIACEAE									
Tabebuia rigida	st/lf	–	–	–	–	+	gr/bk	–	(35–43)
BROMELIACEAE									
Vriesea sintenisii	wp	–	–	–	–	–	gr	–	
CAMPANULACEAE									
Lobelia portoricensis	st/lf	+	+	+	+	–	gr	–	(44–54)
CELASTRACEAE									
Torralbasia cuneifolia	st/lf	–	–	–	–	+	br	–	
CYPERACEAE									
Carex polystachya	st/lf	–	–	–	–	–	br	–	(55–62)
Eleocharis yunquensis	wp	–	–	–	–	–	–	–	(63)
Scleria secans	wp	–	–	–	–	–	br	–	
CYRILLACEAE									
Cyrilla racemiflora	st/lf	–	–	–	–	+	bk	–	
ERICACEAE									
Hornemannia racemosa	st/lf	–	–	–	–	+	gr/bk	–	
GESNERIACEAE									
Gesneria sintenisii	st/lf	–	–	–	–	+	br	–	(64)
GRAMINEAE									
Arthrostylidium sarmentosum	st/lf	+	+	–	–	–	gr	–	
GUTTIFERAE									
Clusia grisebachiana	st/lf	–	–	–	–	+	bk	–	(65)
LAURACEAE									
Ocotea spathulata	wp	–	–	–	–	+	br	–	(66–72)
MARCGRAVIACEAE									
Marcgravia sintenisii	st/lf	–	–	–	–	+	br	–	

MELASTOMATACEAE								
Calycogonium squamulosum	st/lf	−	−	−	−	+	gr/bk	−	
Mecranium amygdalinum	st/lf	−	−	−	−	+	gr/bk	−	
Miconia foveolata	st/lf	−	−	−	−	+	gr/bk	−	
Miconia pycnoneura	st/lf	−	−	−	−	+	br	−	
MELIACEAE								
Trichilia pallida	st/lf	+	+	+	−	+	bk	−	(77)
MORACEAE								
Cecropia peltata	lf	−	−	−	−	+	br	−	(78,79)
MYRSINACEAE								
Ardisia luquillensis	st/lf	−	−	−	−	+	bk	−	(80–84)
MYRTACEAE								
Calyptranthes krugii	st/lf	−	−	−	−	+	br	−	
Eugenia borinquensis	st/lf	−	−	−	−	+	bk	−	(85–90)
OLEACEAE								
Haenianthus salicifolius var. *obovatus*	st/lf	−	−	−	−	+	bk	−	
RUBIACEAE								
Hillia parasitica	st/lf	+	+	+	+	−	−	−	(91)
Psychotria berteriana	st/lf	+	+	+	−	+	gr/bk	+	(92–95)
Rondeletia portoricensis	st/lf	−	−	−	−	+	bk	−	(96)
SAPOTACEAE								
Micropholis garciniaefolia	st/lf	−	−	−	−	+	bk	−	
SYMPLOCACEAE								
Symplocos micrantha	st/lf	−	−	−	−	+	br	−	(97–100)
THEACEAE								
Cleyera albopunctata	st/lf	−	−	−	−	+	gr/bk	−	
THYMELAEACEAE								
Daphnopsis philippiana	st/lf	+	+	−	+	+	gr/bk	−	
URTICACEAE								
Pilea yunquensis	wp	−	−	−	−	−	−	−	(101–103)
ZINGIBERACEAE								
Renealmia antillarum	wp	−	−	−	−	+	−	+	

Key: [a]wp = whole plant, st/lf = stems and leaves; [b]Wall *et al.* procedure (1), based on confirmatory test; [c]Mayer's reagent (4); [d]Silicotungstic acid (5); [e]Farnsworth and Euler procedure (3); [f]br = brown, gr/bk = green-black, bk = black, gr = green.

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